STUDIES ON GROWTH AND VARIATION IN LARGE ANIMALS

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CONTENTS

INTRODUCTION

The hopes which accompanied the birth and infancy of the science of genetics have somewhat faded. Expectations based on the early Mendelian experiments that animal breeding would be revolutionized and progress accelerated proved ill-founded when applied to economic characters with a complex mode of inheritance. Time and effort have since shown that a complete genetic analysis of most of these qualities is hardly possible and perhaps not even desirable. The animal geneticist is therefore obliged to think in terms of gene combinations rather than of genes, and to abandon attempts at factorial analysis.

This change of thought model with its associated statistical techniques does not bring the immediate problem of genetic research with domestic animals any nearer a solution. That problem is the recognition, measurement and exploitation of genetic variation. It is the old problem of relating phenotype to genotype but expanded into the more general question of the interaction of genes not only with external environment, but also with the internal environment set up by the activities of other genes.

As a purely genetic problem this would be exceedingly involved, but it is rendered still more difficult by the power of environment to produce variations indistinguishable/

indistinguishable from those arising from gene differences. The search for these differences therefore requires a simultaneous study of the effects of environment with the object of discriminating between the two types of variation. It would obviously be of great advantage if either genetic constitution or environment could be kept constant, and attempts to do this are frequently made. Even if these attempts did not usually demand more time and expense than most workers can provide, they would, if successful, still leave unsolved the very important problem of the interaction of heredity and environment in the practical breeding of animals in which neither is constant. As an example the variation in the milk production of sows may be cited. Here it is clearly of moment to identify those animals which are genetically superior not so much under standard conditions as under the changing conditions of humidity, temperature, housing and feeding characteristic of most piggeries.

The following pages contain some of the results secured so far in an attempt to assist in the solution of the general problem of the geneticist dealing with domestic animals. Most of the material has been obtained from the pigs of the Institute of Animal Genetics in Edinburgh, but as the field of research is not peculiar to the pig, opportunities for advancing the work with material from other sources have been gladly taken./

Three major subdivisions of the studies may be recognized. The first is concerned with the search for sources of variation in birth weights, a subject which derives its interest from its bearing on the survival and growth of the new-born. Breeding experiments with pigs have still to be completed, but an effort to alter birth weight by raising the plane of nutrition of the sows is described. Naturally occurring variation in the birth weights of sheep and of humans has been studied with extensive material suitable for examining the influence of environmental factors.

The second subdivision includes the results of research into the growth of pigs and sheep from birth to weaning, that is, during the time when the milk production of their dams is of special significance. Here also the object has been to measure variation and to determine what proportion of it may be attributed to heredity.

The third subdivision contains accounts of investigations into the post-weaning growth of pigs. During their progress toward bacon weight, pigs trace out growth curves which vary not only from litter to litter but also from one litter-mate to another. These inequalities of performance provide the raw material for selection aiming at the ideals of early maturity and ever more rapid growth. But before they can be confidently /

confidently used for that purpose, they must be described in terms of heritable characters. Thus the efficient planning and conduct of breeding programmes no less than the practical application of Testing Station results, depends upon the definition and measurement of genetic differences in growth rate. With this in mind, an extensive study has been made of the variation found in a single herd with a standard system of management. Further, recent developments have suggested that growth rate has an important bearing on the body proportions of the marketed animal, so that it has been of interest to compare the observed differences in growth rate with the corresponding variations in carcass quality.

Owing to the nature of the materials, the various phases of the attack on these problems have not been completed in the order in which they were conceived. In several instances the results of breeding experiments which would provide valuable complementary data are not yet available. It is hoped, however, that what has been learnt of variation in these studies will aid the interpretation and enhance the value of the finished work.

DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH.

THE GROWTH-RATE OF LAMBS IN CANTERBURY.

A PRELIMINARY STUDY OF THE VARIATION IN THE GROWTH-RATE OF LAMBS IN CANTERBURY.

BY

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Contents.

(1) Summary.

(1) Factors affecting the birth-weight of pure-bred and cross-bred lambs in Canterbury are discussed. It is shown that for the 1933 lambing season purebred Southdown and Romney Cross by Southdown ram lambs were heavier than ewe lambs, whereas purebred English Leicesters did not differ with sex. Two-tooth ewes in general had lighter lambs than older ewes. There is evidence to show that as the lambing season progressed birth-weights increased. The association which existed between birth-weight of lamb and weight of ewe at lambing suggests that these increases are due partly to improved nutrition of the ewes.

The difference in birth-weight between ram and ewe lambs from RX* ewes on light country was found to be negligible if the ewes were lighter than 100 lb. at lambing. It was quite marked when the ewes were 130 lb. or more.

(2) At 70 days old English Leicester ram lambs were still the same weight as the ewe lambs, but the lambs of two-tooth ewes were smaller than those of older ewes. Almost the reverse was true in Southdowns, among which sex, but not age of ewe, had a marked influence on weight. The RX by SD lambs, the males of which had been castrated, did not show any real difference between the sexes.

(3) At 130 days old the weights of English Leicester lambs showed that sex as well as age of ewe was associated with differences in weight, although previously it was not. The Southdown lambs from two-tooth ewes were practically as heavy as those from older ewes, but ram lambs were heavier than ewe lambs.

(4) A correlation was found between the weights at birth and at 70 days which was less than that between the weights at 70 and 130 days old. The birth-weight of the Southdown lambs was a less-reliable indication of their later growth than was the birth-weight of English Leicester lambs.

(5) The variability in weight of lambs at different ages, and its effect on the number of animals required for experimental purposes, is discussed. No serious attempt has been made to place interpretations on the results which have been presented. Such an attempt is considered premature not only because the analysis of variation in growth-rates is far from complete, but because the extent of purely seasonal influences cannot be judged from one year's figures. The necessity in either breeding or experimental work of knowing the nature and importance of the causes of normal variation makes further investigation of them most desirable. The method of analysing variance has been found very useful and its wider use would probably affect considerably the designing of experiments with animals and the value of the results.

(2) INTRODUCTION.

Measurements in any flock reveal in no uncertain way that sheep rarely resemble each other closely in more than a very few respects. This variation may be regarded from some points of view as a disadvantage, but it may be turned to useful account. Apart from being a source of improvements in breeding and management, it provides a subject for study which can yield useful information concerning the growth and production of sheep.

All variations may be related to some antecedent causes. The identification of these causes is necessary to provide a reliable basis for improved breeding and feeding practice, and much agricultural research is designed to achieve this purpose. The mature sheep, however, represents the end product of the reactions of a certain hereditary complex with many environmental influences. If either the inheritance or the environment alters, the end product will be different, and, since it is very unusual for either to be identical for any two sheep, the task of dissociating the various effects is no light one. Any attempt to breed for production or to feed and manage a flock so that the incidence of disease is low and net returns high should include some attack on this task in order to avoid confusion of effects. For instance, it would be inadvisable to judge the genotype of a dairy bull from the records of his daughters unless these had been corrected for age, service period, feeding, and so on. Similarly, growth-rates of lambs not considered in the light of sex, time of birth, or age of ewe would give a misleading indication of the value of a ram for fat-lamb production.

* RX=Romney crossbred; S.D.=Purebred Southdown.

A complete analysis of the relative effects of hereditary and environmental factors is still far from being achieved, but much can be done towards accurate interpretation of observed facts. The application of statistical method to data from experiments with animals undoubtedly sheds more light on their significance, but if the nature and amount of the data to be collected were determined with more reference to their subsequent statistical treatment more information might often be derived from experiments.

Some of the major causes of variation in growth-rate of lambs have been dealt with by Hammond(1). If allowance is made for each of these, there is difficulty in securing, except for rather gross differences, information which is statistically sound from small mobs of sheep. Just how many sheep would be required to show reliably the existence of a difference will depend on the variability due to causes other than those under examination. It is proposed to deal further with this point.

Observations in Canterbury upon a fairly considerable number of ewes and lambs have recently been made to obtain records of performance. These permit an investigation of the degree to which variables such as age and weight of ewe, time of birth, and locality affect the growth, production, and resistance to disease of lambs and ewes. The close connection which has already been found (Leslie(2)) between feeding, production, and diseases of ewes and lambs in Canterbury points strongly to the necessity for keeping records of experimental sheep so that past may assist in explaining present performance. There is therefore probably sufficient justification for the following attempt to estimate the relative effects of certain known factors which modify growth and production. It is hoped also to assist the comparison and selection of rams by the discovery of suitable adjustments to reduce the present difficulty in comparing small progenies.

(3) GENERAL.

Observations have been made on both purebred and crossbred ewe flocks. From approximately 800 Romney cross ewes and their lambs running on light land, performance records for the past two years have been collected for the purpose of research into animal-health problems by the Veterinary Department of Canterbury Agricultural College. Full accounts of the climatic and soil conditions, husbandry practice and methods of experimentation have already been given by Leslie(2, 3), and will not be repeated.

Weighings have been made at birth and three times thereafter of tagged lambs in purebred English Leicester and Southdown flocks. These sheep were subjected to practically the same climatic conditions as the crossbreds, but obtained better feed. They are run on medium to heavy land and receive a comparative abundance of feed at all times. Although the sire is known for the majority of lambs, it has not been considered desirable to present the inconclusive data which can be derived from one year's records. Discussion of variation in twins will also be excluded from this paper.

The English Leicester flock has been inbred fairly intensively for the past fifteen years. During this time only three sires, already related to the flock, have been introduced. This is not true to nearly the same extent in the Southdowns.

Shearing took place in the third week of November, and weaning in the third week of January for both the purebred and crossbred flocks. At tailing, the ram lambs in the purebred flocks were not castrated.

(4) CLIMATIC AND FEED CONDITIONS DURING THE YEAR (1933–34).

The winter of 1933 was not particularly severe but partial failure of the turnip crop necessitated dry feeding with chaff and hay in addition to rationed turnip tops for the crossbred ewes until well into lambing. During the latter half of lambing the growth of grass improved and the later ewes lambed in better condition. All ewes were put on to green-feed oats after lambing. As grass became available they were shifted from the oats. The purebreds received grass supplemented with mangels, hay, chaff, and molasses. They lambed on good grass and continued thereon until the last weighing dealt with in this paper. The lambing season was popularly regarded as a good one. Weather conditions were at no time very severe.

The last ten days of August were for the most part overcast, but, except for four rainy spells, September was fine and mild. No very cold nights were experienced during the whole lambing season.

About the beginning of November continued dry weather caused a shortage of grass on light country, and ewes and lambs suffered a check. There is no evidence that this occurred on heavier land to any appreciable extent.

(5) VARIATION IN BIRTH-WEIGHTS.

(*a*) *Technique.*—All lambs were weighed and tagged as soon as possible after birth. With large flocks it is not practicable to handle all lambs at any constant interval after birth, so that two sources of error are introduced. For some time the lambs are wet with amniotic fluid, and gradually lose weight as it dries. Any suckling of the ewe before weighing will counteract and possibly outweigh this loss. If ten to twenty-four hours elapse before weighing there is an appreciable error introduced by the amount of milk obtained by the lamb. Weighings at short intervals after birth have shown that there is usually a slight decrease in weight, followed by an increase of anything up to 1 lb. at the end of twenty-four hours. This agrees with the experience of Sidey (4).

The field practice followed was to weigh lambs throughout the day. Since most of the lambs are dropped during the night they would be from three to twelve hours old before weighing. Consequently mean birth-weights are possibly slightly higher than the real "dry weight at birth."

Further, the recording of weights to the nearest tenth of a pound, as was done, does not necessarily indicate considerable accuracy in measuring the birth-weights. It may well be assumed that for a reasonably large number of lambs any discrepancy would be practically the same for different groups and that comparisons between them on a basis of observed weights would be valid. This assumption, however, may not be justified, since Romney cross ewes have been found with lambs which at twenty-four hours old were the same weight as at birth. This may be due to failure of the lambs to suckle,

but, if it could be attributed in part at least to failure of the ewe to milk well immediately after parturition, then such a characteristic for a strain or flock as a whole is conceivable—*e.g.*, for Southdowns, or for poorly nourished two-tooth ewes. Birth-weights would then be biased in favour of better milking-ewes.

Richter and Brauer, quoted by Hammond (*loc. cit.*) found that lambs took on the average 1·7 days to regain the weight lost after birth from evaporation of moisture. This is considerably in excess of the time required by the lambs examined in Canterbury.

(*b*) *Effect of Season.*—Since it has been shown that the birth-weight of lambs may be modified by the condition of the ewe at lambing, mean birth-weights might be expected to vary from season to season. The influence of different planes of nutrition, however, need not necessarily have the same effect. Breeds differ in ability to adjust themselves to a shortage of feed, and individual ewes existing on a diet deficient in any way may not sacrifice themselves equally for the sake of their lambs. Seasonal changes may therefore be reflected to different extents in the birth-weight of lambs.

Table 1 shows the mean birth-weights of single lambs obtained in Canterbury during the last two years.

TABLE 1.—MEAN BIRTH-WEIGHT OF SINGLE LAMBS (BOTH SEXES) FOR 1932 AND 1933.

Breed.		Year.	Mean Birth-weight.	No.	Remarks.
Ewe.	Ram.				
			A. For Light Land.		
			lb.		
RX	SD	1932	9·78	571	Wintered on turnips and chaff.
RX	SD	1933	9·34	405	Shortage of turnips in winter.
			B. For Medium and Heavy Land.		
RX	SD	1932	10·18	74	
RX	SD	1933	9·43	51	
EL	EL	1933	9·84	70	Well wintered.
SD	SD	1933	8·22	65	Well wintered.
R	R	1933	10·02	31	Well wintered.

EL = Purebred English Leicester; R = Purebred Romney; SD = Purebred Southdown; RX = Crossbred Romney.

There is some evidence of a seasonal influence which is probably related to the winter feed available. It is noticeable for the RX × SD lambs on light country and for similar lambs on heavy country for 1932–33. Hammond has found a seasonal variation over a much longer period of years which he attributes mainly to an influence of rainfall on available feed. A comparison between the mean birth-weights of the comparable lambs (RX × SD) shows slightly heavier weights for the lambs raised on the better land. This difference is probably due to the same cause as operates from season to season.

The value of these figures is strictly limited because they represent only the relation between general husbandry conditions and birth-weight, and for most purposes, experimental or otherwise, this is insufficient. The explanation of the seasonal and local variation must be sought from a more detailed study.

Inset—Growth-rate of Lambs.

Such detailed studies have been facilitated in recent years by the introduction of statistical method designed to extract the maximum amount of information from observed data. The analysis of variance as developed by Fisher(5) has proved very useful. Examples illustrating its use have been published by Fisher (*loc. cit.*), Yates(6), and Dunlop(7).

(c) *Factors affecting Birth-weight.*—The following factors which are known to influence birth-weight will be examined in their relation to Canterbury conditions: Sex of lamb; age of ewe; time of birth; weight of ewe; winter feeding.

Sex of Lamb and Age of Ewe.—It is common knowledge that ram or wether lambs have a higher average weight than ewe lambs, and that two-tooth ewes as a rule do not produce such well-grown lambs as older ewes. The magnitude of these differences for the 1933 season is shown in the following analysis of the variance occurring in two flocks of purebred ewes. In these analyses it will be noted that all single lambs from each flock have been used to obtain an estimate of the proportions which variation in birth-weight due to sex bears to variation caused by age of ewe within each sex group, and to residual variation. This latter is a measure of the variation due to all causes not specified—*i.e.*, heredity, weight of ewe, accidents, &c.

TABLE II.—COMPARISON OF VARIANCE DUE TO SEX OF LAMB AND AGE OF EWE WITH THAT DUE TO ALL OTHER CAUSES.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOG_e	*z*	P
			Southdown Lambs.					
Males ..	7·74 (7)	8·88 (24)	Sex ..	1	9·44	1·123	0·965	0·01
Females	7·50 (16)	8·17 (18)	Age of ewe	1	10·76	1·188	1·030	<0·01
Mean ..	7·57 (23)	8·57 (42)	Error ..	62	1·37	0·158	..	..
			Total ..	64	1·64	..	..	..
			English Leicester Lambs.					
Males ..	9·16 (11)	10·31 (27)	Sex ..	1	1·49	0·199	0·040	..
Females	9·10 (14)	10·13 (18)	Ewe's age	1	18·31	1·454	1·295	<0·01
Mean ..	9·12 (25)	10·24 (45)	Error ..	67	1·38	0·159	..	..
			Total ..	69	1·62	..	..	..

NOTE.—The total variance, which is obtained by adding the squares of the differences of each lamb-weight from the mean weight of all lambs, is divisible into portions attributable to sex of lamb, age of ewe, random error, &c. These portions when divided by the corresponding degrees of freedom (D.F.) give the figures in the column headed "mean square." These mean squares are compared with the aid of the *z* transformation. Half the natural logarithm of each mean square is calculated, and the value of *z* is found by difference. To compare, for example, the variance due to sex of lamb with that due to random error in birth-weight of Southdown lambs, *z* is obtained from the values of ½ LOG_e (1·123–0·158) = 0·965. The probability (P) that this value could arise by chance is found from Fisher's table of *z*. If P is less than 5 per cent. (0·05)—that is, if the chances are more than 20 to 1 against this value of *z* being a purely accidental one, the difference in observed weights is regarded as significant.
The numbers of lambs from which the mean weights were calculated are shown in brackets.

According to the table of *z* the chances are about 100 : 1 that the difference in mean birth-weights of ram and ewe lambs in the Southdown flock is a real one. This is in accordance with the usual belief. In the English Leicester flock, however, the variance due to sex

(1·49) is very little greater than that due to random variance (1·38) and, on this evidence, there are no grounds for concluding that there is any difference between the sexes in weight at birth. In both flocks the age of the ewe is responsible for a greater variance than sex.

In the English Leicester flock about 14 per cent. of the variance may be attributed to age of ewe, while in the Southdowns the corresponding figure is about 9 per cent. The error-variance has been reduced to 85 per cent. of the total variance in both flocks by eliminating sex and age of ewe. It may be noted here that the lambs of two-tooth ewes differ less in weight with sex than those of older ewes.

Although there is evidence to show that birth-weight may increase with successive lambs at least until the ewe is full-mouthed the only distinction which has been made above is that between two-tooths and older ewes. It is probable, however, that further analysis would reduce the error-variance still more.

Sex of Lamb and Winter Feeding.—Much the same conclusion regarding the effect of sex can be drawn from the following table showing a similar analysis of variance for lambs from Romney Cross ewes on light land.

Although these ewes have been fed in two different ways during winter the variance due to sex is comparable with the error-variance as before. Treatment has been eliminated in place of age of ewe. As no two-tooth ewes were present the comparison of sex and error-variances for the different localities is regarded as valid for the feeding and husbandry practices concerned.

TABLE III.

Lambs.	Treatment "A."	Treatment "B."	Variance.	D.F.	Mean SQ	½ LOG_e	*z*	P
Males ..	10·81 (39)	9·36 (52)	Sex ..	1	12·75	1·273	0·906	>0·01
Females	9·80 (65)	9·00 (44)	Treatment	1	64·15	2·081	1·714	<0·01
			Error ..	197	2·08	0·367	..	..
			Total ..	199	2·45	..	..	..

The odds that there is an effect of sex over the whole flock are a little lower than 100 : 1. If the effect of sex had been calculated on the treatment groups separately it would have been much greater. The considerable difference between males and females in the group getting treatment "A" has been somewhat reduced by combining them with those receiving treatment "B."

Unless the groups under treatments "A" and "B" differed in respect of any other factors affecting birth-weight, there must have been interactions between treatment and birth-weight which were different in the groups. In these groups the total variance has been reduced by about 3 per cent. by eliminating variance due to sex.

Time of Birth.—Hammond gives figures for three seasons showing that early lambs (singles) were about 2·2 lb. lighter at one week old than late lambs. To a certain extent this association of time of birth and weight has been found in Canterbury in 1932 and 1933. Mean birth-weights of English Leicester lambs, divided into three

groups according to time of birth, showed significant differences. The estimation of variance due to this cause resulted in a further reduction of error-variance from 1·38 to 1·25.

Weight of Ewe.—Whilst the association between weight at birth and time of birth may be accepted, the underlying causes of this are not apparent from lamb-weights alone. It has been suggested that the condition of the ewe improves as the spring grass becomes available, and that the lamb benefits as a result. An investigation of this point is possible if the weights of ewes at lambing are known.

The weighing of many ewes just before or after each lambs is impracticable. It is possible, however, to weigh all ewes just before lambing commences, and then to weigh unlambed ewes at some time during the lambing season. This was done in the flock of RX ewes. From these two weighings the increase in weight could be calculated. This was found to be practically the same for ewes of all weights. The actual weight of ewes at lambing was then calculated from the live weight increase per day so determined, the date of lambing, and its weight at the last weighing, and includes the weight of the lamb.

Although the weights of individual ewes increased as lambing proceeded, it does not follow that the mean weights of ewes lambing during successive periods should show a progressive increase. During the 1933 lambing season the mean weights shown in Table IV of ewes at lambing were calculated by the above method.

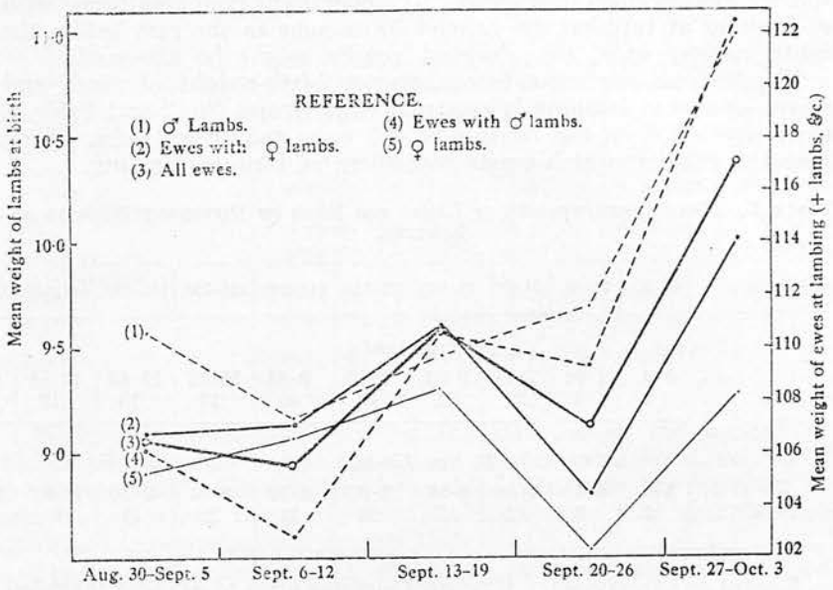
TABLE IV.—MEAN WEIGHTS OF EWES AND LAMBS AT LAMBING FOR WEEKLY PERIODS.

——	First Period.	Second Period.	Third Period.	Fourth Period.	Fifth Period.
Weight of ewes with male lambs	106·0 (59)	102·8 (30)	110·7 (65)	109·3 (20)	122·4 (17)
Birth-weight of male lambs	9·59 (59)	9·17 (30)	9·48 (65)	9·71 (20)	11·01 (17)
Weight of ewes with female lambs	106·9 (54)	107·2 (47)	110·9 (66)	104·4 (18)	114·1 (29)
Birth-weight of female lambs	8·92 (54)	9·07 (47)	9·31 (66)	8·54 (18)	9·28 (29)
Mean weight, all ewes ..	106·4	105·5	110·8	107·0	117·1
Mean weight, all lambs ..	9·27	9·07	9·39	9·16	9·92

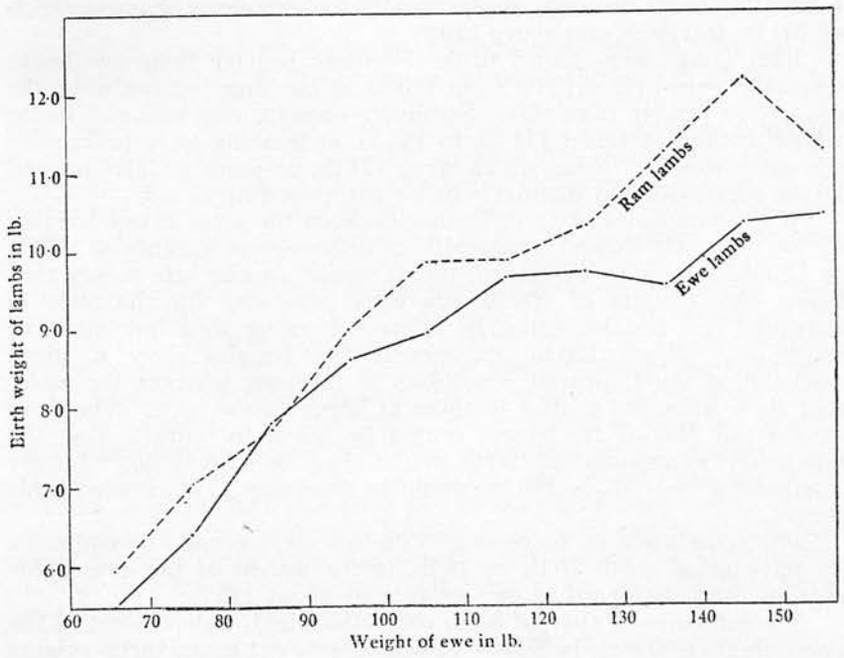
First period, 30th August to 5th September; second period, 5th to 12th September; third period, 13th to 19th September; fourth period, 20th to 26th September; fifth period, 27th September to 3rd October.

It will be noted that there is a slight drop from the first period to the second, and a much larger one from the third to the fourth. This is also shown in Graph No. 1. Consequently, if there is a close connection between birth-weight of lamb and weight of ewe, a continuous increase in birth-weight of lambs could not be expected with the passage of time.

Just why the mean weight of ewes should not show a regular increase corresponding to that of any one ewe is doubtful. A possible explanation is suggested by the fact that the two decreases in weight are separated by a period approximately equal to that



GRAPH No. 1.—The mean weights of ewes and lambs at lambing for weekly periods.



GRAPH No. 2.—The mean birth-weights of lambs for ewes of different weights at lambing.

between heat periods in the ewe. If under light land conditions with no flushing at tupping the heavier ewes come to the ram before the lighter poorer ones, the observed results might be expected.

The general correspondence between birth-weight of lamb and weight of ewe at lambing is apparent from Graph No. 2 and Table V which are based on the records of 432 ewes and their lambs. They show the relation which exists regardless of time of lambing.

TABLE V.—MEAN BIRTH-WEIGHTS OF LAMBS FOR EWES OF DIFFERENT WEIGHTS AT LAMBING.

Ewe-weight (lb.).	61–70.	71–80.	81–90.	91–100.	101–110.	111–120.	121–130.	131–140.	141–150.	151-
A. Ram Lambs.										
Mean	5·9	7·08	7·74	9·05	9·85	9·84	10·32	11·25	12·18	11·
Number	1	4	21	42	46	45	17	13	12	1
B. Ewe Lambs.										
Mean	5·5	6·4	7·86	8·66	8·99	9·72	9·76	9·55	10·3	10·
Number	2	3	22	47	53	51	29	13	9	1

Except for thirty-eight English Leicester ewes of all ages included to show the relation at low ewe-weights, the ewes are four-, six-, and eight-tooth Romney Cross. It is apparent that heavy ewes give birth as a rule to heavy lambs. While this may apply to both male and female lambs, it does not apply equally to both sexes at ewe-weights of 101 lb. to 110 lb. and above 120 lb.

Ram lambs were found to be definitely heavier than ewe lambs when the ewes weighed 100 lb. to 110 lb. at lambing, but not when the ewes were lighter than this. Strangely enough, ram and ewe lambs whose mothers weighed 111 lb. to 120 lb. at lambing were practically the same weight. Ewes which were 131 lb. or more at lambing had lambs which differed distinctly in weight according to sex.

Why there should be a difference between the sexes at ewe weights of 100 lb. to 110 lb. and practically no difference at weights of 110 lb. to 120 lb. cannot be explained, but it would appear safe to say that below ewe weights of 100 lb. the usual tendency for the male to outweigh the female cannot be expressed owing to a low plane of nutrition. Above 120 lb. ewe-weight the females show a slight response to the improved conditions in the ewe, whereas the males still show increases similar to those at lower ewe-weights. The drop at the tail end of the graph cannot be taken to indicate that the maximum expression of birth-weight has been reached. Larger numbers of ewes above 150 lb. would be necessary to show where this occurs.

For male lambs an increase of 1 lb. in weight usually accompanies an increase of about 10 lb. to 15 lb. in the weight of the ewe. This applies for females up to ewe-weights of about 115 lb.

The influence of time of birth on birth-weight, independent of the ewe-weight, is shown in Table VI which sets out mean birth-weights of lambs from ewes of the same weight at lambing in the five periods into which the lambing period was divided.

TABLE VI.—MEAN BIRTH-WEIGHTS OF LAMBS FROM EWES OF EQUAL WEIGHT AT LAMBING.

—	30th August to 5th September.	6th to 12th September.	13th to 19th September.	20th to 26th September.	27th September to 3rd October.
Ewes 105–110 lb.—					
Males	9·67 (7)	9·60 (3)	9·25 (13)	8·73 (3)	11·65 (2)
Females	8·59 (7)	8·73 (9)	8·97 (10)	9·56 (5)	9·82 (5)
Ewes 111–115 lb.—					
Males	9·78 (9)	9·45 (4)	9·57 (6)	10·33 (3)	11·17 (3)
Females	9·94 (9)	9·80 (7)	9·96 (7)	..	9·35 (2)
Ewes 105–115 lb.—					
Males	9·73 (16)	9·51 (7)	9·35 (19)	9·53 (6)	11·36 (5)
Females	9·35 (16)	9·20 (16)	9·38 (17)	9·56 (5)	9·69 (7)
All lambs	9·54 (32)	9·30 (23)	9·36 (36)	9·55 (11)	10·38 (12)

With the possible exception of the last period, the means for the various periods do not show any greater variation than might be expected with the numbers available. Much of the increase in birth-weight which takes place as lambing passes may therefore be attributed to improved condition of the ewe.

The possibility that weight of the ewe influences the birth-weight of the lamb to an extent which is modified by the age of the ewe has not yet been investigated.

(6) VARIATION IN WEIGHTS AT DIFFERENT TIMES UP TO WEANING.

In order to place all lambs on a comparable basis subsequent to birth it has been found necessary to calculate the weight at definite ages from observed weights. Since most weights are recorded on particular days the actual ages of the lambs vary and the weights are not comparable. The probable weights at a given age—*e.g.*, 10, 15, 70, or 130 days—have therefore been calculated by adding to or subtracting from the observed weight an amount equal to the live-weight increase per day, shown up to day of weighing times the number of days short of or in excess of the required age. This would be quite sound only if the average live-weight increase per day used were a true indication of the growth-rate between the actual age at weighing and the standard age. Growth-curves for lambs weighed at short intervals (10 days) show that the live-weight increase per day is practically constant at least up to 70 days, provided the feed-supply is adequate. So far, then, as calculated weights at 10, 15, and 70 days are concerned, the error introduced would be small. In any case, the growth-rate will not alter greatly during the few days by which most lambs differ from the standard, and the error, therefore, will be correspondingly small. For each standard age the weight was calculated from the growth-rate between the weighing at this time and the previous one. All calculations which follow have been based only on healthy lambs.

(*a*) *Weight at Tailing-time.*—Most English Leicester lambs were tailed at about 10 days old and the Southdown lambs at about 15 days. The following mean weights and variances were obtained.

TABLE VII.—MEAN WEIGHTS AND VARIANCE AT TEN DAYS FOR ENGLISH LEICESTER LAMBS, AND AT FIFTEEN DAYS FOR SOUTHDOWN LAMBS.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOG_e	z	P
			A. English Leicester Lambs.					
Males ..	15·32 (10)	17·37 (27)	Sex ..	1	24·10	1·59	0·76	<0·05
Females	14·29 (14)	16·68 (18)	Age of ewe	1	76·03	2·17	1·34	<0·01
Mean ..	14·72 (24)	17·10 (45)	Error ..	66	5·21	0·83	..	..
			Total ..	68	5·53	..	..	..
			B. Southdown Lambs.					
Males ..	15·27 (6)	16·74 (23)	Sex ..	1	22·54	1·56	0·61	>0·05
Females	14·34 (16)	16·04 (18)	Age of ewe	1	34·88	1·78	0·83	<0·05
Mean ..	14·59 (22)	16·43 (41)	Error ..	60	6·66	0·95	..	..
			Total ..	62	7·37	..	..	..

It will be noted that about 20 per cent. of the total variance in English Leicester flock at this age may be attributed to differences in sex of lamb and age of ewe, whereas the corresponding figure for the Southdowns is 10 per cent.

It is clear that both ram and ewe lambs from two-tooth ewes are lighter than those from older ewes, just as they were at birth. At 10 days, however, the English Leicester ram lambs appear to have exceeded the ewe lambs in weight, although they were equal at birth. On the other hand, the difference in weight between the sexes among Southdown lambs is not as marked at 15 days as at birth. There would appear to be less than twenty chances to one that the difference shown by the means is not a chance one. In view of the difference which will be established between the sexes at 70 days old, it would be safer to suppose that the apparently slighter effect of sex at 15 days is an outcome of the increased variance due to a variety of causes such as content of stomach, different growth-rates, &c.

(*b*) *Weight at 70 Days.*—This corresponds approximately to weight at shearing-time.

TABLE VIII.—MEAN WEIGHTS AND VARIANCE AT SEVENTY DAYS FOR ENGLISH LEICESTER LAMBS.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOG_e	z	P
Males ..	46·38 (10)	53·38 (25)	Sex ..	1	114·17	2·37	0·49	>0·05
Females	46·34 (13)	50·48 (18)	Age of ewe	1	479·70	3·09	1·21	<0·01
Mean ..	46·36 (23)	52·17 (43)	Error ..	63	42·54	1·87	..	..
			Total ..	65	50·37	..	..	..

The observed value of $z = 0{\cdot}49$, is less than the value of 0·69 demanded for P = 0·05, and the effect of sex cannot be regarded as

significant. The difference of 2·9 lb. between male and female lambs of older ewes taken separately is not significant.

Mean weight of males 53·38 ± 1·38
50·48 ± 1·49
Difference 2·90 ± 2·03

The difference is not much greater than its standard error.

A comparison of the error-variance shown in Table XII with that found by calculating the weight at standard age (70 days) using a correction for lambs older than 70 days based on the growth-rate from shearing till weaning time showed no significant difference.

	Mean SQ.	LOG_e.	1/n.
Error variance (Table XII) ..	42·54	3·75	0·01587
Error variance (Alternative Method)	41·69	3·73	0·01587
Difference	..	0·02	..
	z =	0·01	

Variance of $z = 0{\cdot}01587$
SD of $z = 0{\cdot}126$

The comparable figures for the Southdown flock are as follows:—

TABLE IX.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOG_e	z	P
Males ..	48·40 (6)	49·17 (23)	Sex ..	1	249·56	2·76	1·03	<0·01
Females	43·39 (15)	46·38 (16)	Age of ewe	1	72·28	2·14	0·41	>0·05
Mean ..	44·82 (21)	48·03 (39)	Error ..	57	32·16	1·74	..	..
			Total ..	59	36·52	..	..	..

Among the Southdowns the effect of sex has again become pronounced. Taking males and females separately the age of ewe does not affect the weight of either much more than undetermined causes. Taking males and females together, however, the chances are slightly more than 20 : 1 that the lambs of two-tooths are lighter than those of older ewes.

Under light land conditions the flock which has been considered showed no appreciable difference due to sex. This is shown below.

TABLE X.

Lambs.	Treatment "A."	Treatment "B."	Variance.	D.F.	Mean SQ.	½ LOG_e	z	P
Males ..	51·46 (24)	48·96 (27)	Sex ..	1	23·81	1·59	−0·05	..
Females	49·95 (41)	48·19 (28)	Treatment	1	125·43	2·42	0·78	<0·05
Mean ..	50·51 (65)	48·57 (55)	Error ..	117	26·47	1·64	..	..
			Total ..	119	27·28	..	..	..

The chances are, therefore, that treatment "A" resulted in a superiority of both male and female lambs over those under treatment "B."

(c) *Weight at 130 Days.*—This corresponds to weight at weaning. Between the ages of 70 and 130 days the RX × SD lambs on light land suffered a shortage of feed. The growth-rates fluctuated widely according to the age of the lamb, and the weights at 130 days, which would have little value in this connection, have not been calculated. The purebred lambs went on to weaning-time with a good supply of feed, and the following means and variances were obtained.

TABLE XI.—MEAN WEIGHTS AND VARIANCE AT 130 DAYS FOR ENGLISH LEICESTER LAMBS.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOGe	z	P
Males ..	67·70 (10)	80·49 (25)	Sex ..	1	805·29	3·35	1·16	<0·01
Females	66·46 (13)	72·27 (18)	Age of ewe	1	1422·99	3·63	1·44	<0·01
Mean ..	67·00 (23)	77·05 (43)	Error ..	63	79·22	2·19	..	..
			Total ..	65	111·06	..	..	..

At this age both sex and age of ewe effects are very marked taking the flock as a whole. It is apparent, however, that the sex-variance is mostly due to the superiority in weight of the ram lambs of older ewes. The elimination of variance due to both these factors has reduced the error variance to about 71 per cent. of the total variance.

It will be remembered that there was no definite evidence of any difference between the sexes at birth for either class of ewe among English Leicesters, although perhaps such a difference was foreshadowed by a slight apparent difference in the means at birth and at 70 days. The ram lambs of two-tooth ewes are still very little different from the ewe lambs. Whether this is due to the inability of two-tooth ewes to maintain a sufficient milk-supply to allow their ram lambs to show any faster growth than ewe lambs, or whether the effects of poorer nutrition in utero are responsible, is not apparent from the data. The number of two-tooth ewes with lambs does not permit of an investigation of the possibility that the lambs which are born as heavy as those of older ewes show differences in growth-rate according to sex, provided that milk-supply does not inhibit such a tendency.

That the results are not true for all two-tooth ewes is shown by the figures for the Southdown lambs.

TABLE XII.—MEAN WEIGHTS AND VARIANCE OF SOUTHDOWN LAMBS AT 130 DAYS OLD.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOGe	z	P
Males ..	71·10 (6)	72·19 (22)	Sex ..	1	1005·45	3·46	1·30	<0·01
Females	62·64 (15)	64·59 (16)	Age of ewe	1	45·35	1·91	..	..
Mean ..	65·06 (21)	68·99 (38)	Error ..	56	73·95	2·15	..	..
			Total ..	58	89·52	..	..	..

It has therefore been no disadvantage to these Southdown lambs to be the offspring of two-tooth ewes. The difference between the sexes is most marked. The results in both these respects were quite different in the English Leicester flock.

At birth Southdown lambs showed differences in weight depending on their sex and on the age of their dams. At 70 days sex-differences were still marked, but those due to age of ewe had diminished to non-significance. At 130 days the variance due to this cause was less than that due to "random error."

(7) GROWTH-RATES.

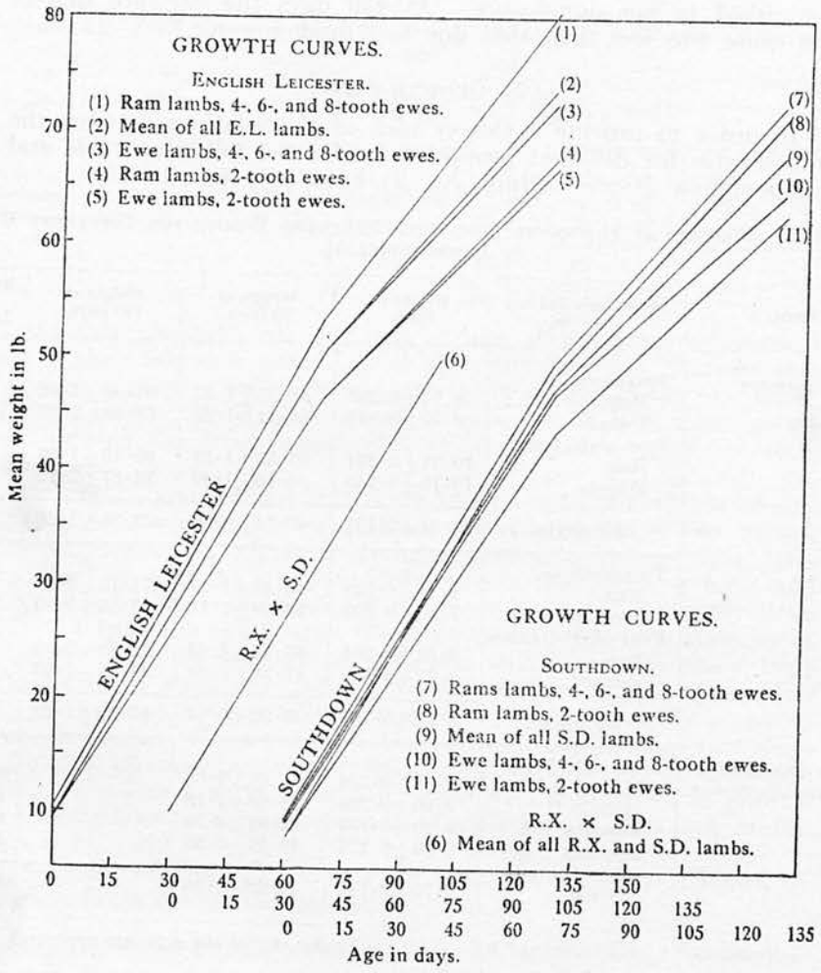
In order to provide a clearer idea of the relations between the growth-rates for different groups of lambs, the following table and corresponding graphs (Graph No. 3) have been constructed.

TABLE XIII.—WEIGHTS AT DIFFERENT AGES WITH STANDARD ERRORS FOR DIFFERENT GROUPS OF LAMBS (SINGLES).

Breed.	Age of Ewe, and Sex of Lamb.	Weight at Birth.	Weight at 70 Days.	Weight at 130 Days.	Number of Lambs.
English Leicester ..	Two-tooth—				
	Male ..	9·16±0·285	46·38±1·52	67·70±1·82	10
	Female ..	9·10±0·259	46·34±1·78	66·46±2·07	13
	Four–eight-tooth—				
	Male ..	10·31±0·261	53·38±1·38	80·49±1·96	25
	Female ..	10·13±0·245	50·48±1·49	72·27±2·17	18
	All singles ..	9·84±0·151	50·14±0·87	73·55±1·29	66
Southdown ..	Two-tooth—				
	Male ..	7·74±0·338	48·40±1·57	71·10±3·21	6
	Female ..	7·50±0·293	43·39±1·27	62·64±1·90	15
	Four–eight-tooth—				
	Male ..	8·88±0·264	49·17±1·43	72·19±2·17	22
	Female ..	8·17±0·240	46·38±1·09	64·59±1·65	16
	All singles ..	8·22±0·160	46·91±0·77	67·59±1·22	59
Romney Crossbred × Purebred Southdown	Four–eight-tooth—				
	Males "A"* ..	10·81±0·259	51·46±1·03	..	39 24†
	Males "B" ..	9·36±0·225	48·96±1·16	..	52 27
	Females, "A"	9·80±0·139	49·95±0·75	..	65 41
	Females, "B"	9·00±0·221	48·19±0·85	..	44 28
	Total ..	9·70±0·110	49·62±0·48	..	200 120

* = Treatment "A" and Treatment "B." † = Number at birth and at 70 days respectively.

Bearing in mind the numbers of lambs used in calculating these means the most striking feature of Graph No. 3 is the close agreement in live-weight increase of all lambs up to 70 days. Even on light land the lambs have grown practically as fast as those on heavier land. The crossbred nature of the lambs may be involved. Also under similar conditions the English Leicester lambs have grown a very little faster than the Southdowns. Whether Southdowns of equal birth-weight to English Leicester would preserve this relation has yet to be discovered.



GRAPH NO. 3.—Growth curves of lambs of different breeds.

From 70 to 130 days the English Leicesters show, on the whole, a smaller decrease in growth-rate than the Southdowns. The relation between the various mean growth-rates calculated from Table XIII is shown below.

TABLE XIV.—MEAN GROWTH-RATES PER DAY.

Breed.	Age of Ewe and Sex of Lamb.	Growth-rate, Birth–70 Days.	Growth-rate, 70–120 Days.	Ratio.
		lb.	lb.	
English Leicester	Two-tooth—			
	Male ..	0·53	0·36	1·47
	Female ..	0·53	0·34	1·56
	Four–eight-tooth—			
	Male ..	0·62	0·45	1·38
	Female ..	0·58	0·36	1·61
	Total, all lambs	0·58	0·39	1·49
Southdown	Two-tooth—			
	Male ..	0·58	0·38	1·53
	Female ..	0·51	0·32	1·59
	Four–eight-tooth—			
	Male ..	0·58	0·38	1·53
	Female ..	0·55	0·30	1·83
	Total, all lambs	0·52	0·35	1·49
Romney Crossbred × Purebred Southdown	Four–eight-tooth—			
	Male ..	0·57	..	..
	Female ..	0·57	..	..
	Total, all lambs	0·57	..	..

(8) RELATION BETWEEN WEIGHTS OF LAMBS AT DIFFERENT AGES.

It will have been noted from the growth curves just examined that, as a rule, those groups of lambs (within a breed) which had a comparatively low mean birth-weight showed relatively low mean-weights at subsequent weighings. There is no measure provided by Table XIII of the degree to which this is true of any one lamb. The importance of knowing at what age lambs may be safely selected for breeding-purposes on a growth-rate basis has been pointed out by Hammond. For experimental work designed to test the effect of a treatment on growth-rate, it is obviously also important. Study of individual records shows that a lamb, which is heavier than another at any one age, is not necessarily heavier than the other when they are older. This is particularly true of young lambs. The chances of malnutrition, disease, or accidents impeding growth are probably greater at this age than they are subsequently. It might be suggested also that birth-weight may be less dependent on the hereditary "growth force" or efficiency in converting environment into body substance than later weights.

Certain correlations which existed between the weights of lambs at birth and at 70 days, and between weights at 70 and 130 days are appended below (Table XV).

TABLE XV.

Group.	r for Weights at Birth and 70 Days.	Number of Lambs.	P	r for Weights at 70 and 130 Days.	Number of Lambs.	P
English Leicester—						
Ram lambs, 2-tooth ewes	0·675	10	<0·04	0·770	10	<0·01
Ewe lambs, 2-tooth ewes	0·495	13	<0·1	0·703	13	<0·01
Ram lambs, 4–8-tooth ewes ..	0·770	25	<0·01	0·908	25	<0·01
Ewe lambs, 4–8-tooth ewes ..	0·636	18	<0·01	0·762	18	<0·01
Combined	0·681	66	<0·01	0·831	66	<0·01
Southdown—						
Ram lambs, 2-tooth ewes ..	..	..	..	..	..	..
Ewe lambs, 2-tooth ewes	0·486	15	<0·1	0·807	15	<0·01
Ram lambs, 4–8-tooth ewes ..	0·396	23	0·05	0·936	22	<0·01
Ewe lambs, 4–8-tooth ewes ..	0·336	16	>0·1	0·891	16	<0·01
Combined	0·40	54	<0·01	0·898	53	<0·01
Romney Crossbred × Purebred Southdown—						
Wether lambs	..	..	..	..	..	..
Treatment "A"	0·768	23	<0·01	..	..	..
Treatment "B"	0·577	27	<0·01	..	..	..
Ewe lambs, "A"	0·544	41	<0·01	..	..	..
Ewe lambs, "B"	0·766	28	<0·01	..	..	..
Combined	0·662	119	<0·01	..	..	..

Apart from the value of 0·495 for ewe lambs of two-tooth ewes the correlations between birth-weight and weight at 70 days among all English Leicester lambs seem fairly similar. However, the value of 0·495 is quite within the range of a normal deviate (for those lambs) from a general value of $r = 0·7$. The corresponding values for Southdown lambs are lower, and practically significantly different.

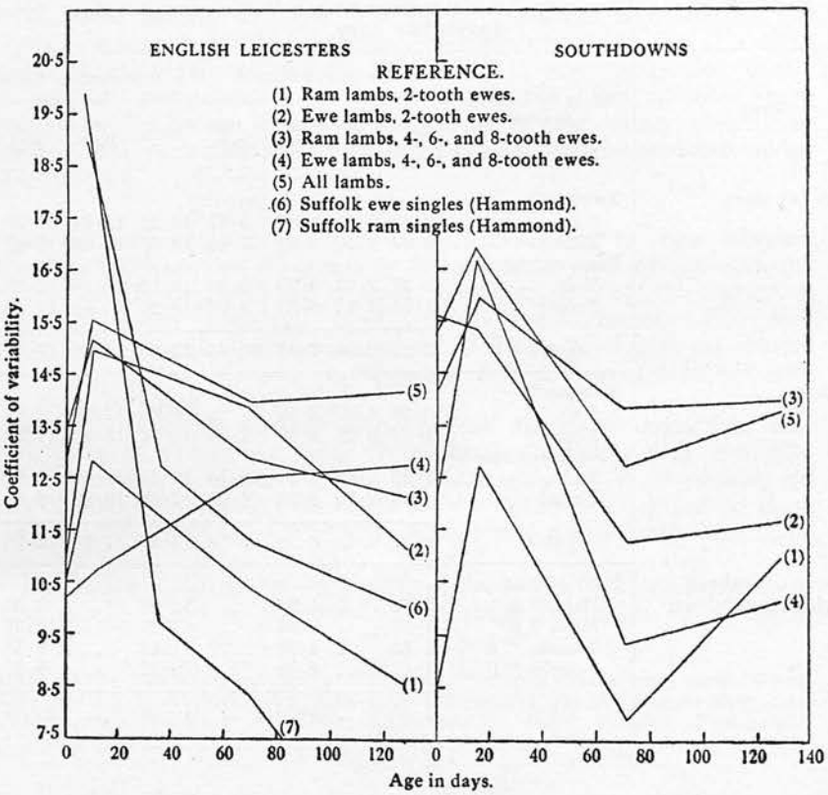
	r	z	1/n–3.
English Leicester lambs	= 0·681	0·831	0·0222
Southdown lambs ..	= 0·40	0·429	0·0185
Difference ..	= ..	0·402 ±	0·202

The difference in value of z is almost twice the standard error, and there is a strong possibility that there was a real difference in the correlations exhibited by the two breeds. The close resemblance of the correlations for both breeds of the weight at 70 days with that at 130 days would indicate that the causes of the apparently low previous correlation in Southdowns have been removed. If recorded birth-weight were for some reason not a good indication of the growth-force, or if the environment—*e.g.*, milk-supply—did not act equally on lambs of the various weight classes, this result might be understandable.

A comparison of the values of r for crossbred and purebred lambs is interesting. The factors affecting the growth of these crossbred-lambs, although probably different in some respects from those acting on the purebred lambs, appear to have had their effects distributed in much the same way as in the English Leicester flock.

For either Southdown or English Leicester lambs it may be assumed that weight at 70 days provides a fairly reliable indication

of growth up to 130 days if the supply of feed, &c., is not greatly different from that in the summer of 1933–34. It may be concluded also that birth-weight is correlated with subsequent growth. The value of the correlation may, however, vary according to breed and other circumstances. Hammond, for example, gives a value of $r = 0·528 \pm 0·088$ for the correlation between weight at one week old and weight at twenty weeks for Suffolk ewe lambs.



GRAPH NO. 4.—The coefficients of variability of mean weights of lambs at different ages.

(9) VARIABILITY IN WEIGHT AT DIFFERENT AGES.

Relative variability as measured by the coefficient of variability does not remain constant during growth. It follows that the response of individuals within a flock to the stimulus of environment does not vary directly as their weight. In other words, if the coefficient of variability increases, light lambs become lighter and heavier ones heavier than they would if the coefficient of variability remained the same. If the coefficient of variability decreases, then for some reason the light ones have caught up somewhat in proportion to their size on the heavy ones. Hammond (*l.c.*), who found that the coefficient of variability decreased with age, subscribes to the view that in sheep reduction in growth-rate may be responsible. This reduction

may be due to shortage of feed or to increasing age. Although the underlying reasons for the alteration in coefficient of variability with time remain obscure, it is clear that even under the same conditions of feed, age, and climate it may alter differently in different flocks. Table XVI and Graph No. 4 illustrate the point. The numbers of lambs in each sub-group are rather small, but in this connection the shortage is not perhaps wholly a disadvantage.

TABLE XVI.—STANDARD DEVIATIONS AND COEFFICIENTS OF VARIABILITY OF MEAN WEIGHTS DIFFERENT AGES.

Breed.	Age of Ewe and Sex of Lamb.	Standard Deviations.				Coefficients of Variability.			
		Birth.	10 Days.	70 Days.	130 Days.	Birth.	10 Days.	70 Days.	13 Da
English Leicester ..	Two-tooth—								
	Male ..	0·95	1·97	4·80	5·77	10·33	12·84	10·35	8·
	Female ..	0·97	2·10	6·43	7·46	10·67	15·00	13·87	11·
	Four-eight-tooth—								
	Male ..	1·36	2·63	6·90	9·80	13·17	15·16	12·93	12·
	Female ..	1·04	1·77	6·33	9·22	10·26	10·62	12·54	12·
	Total ..	1·26	2·54	7·03	10·46	12·85	15·59	14·03	14·
Southdown	Two-tooth—								
	Male ..	0·89	1·95*	3·85	7·86	8·67	12·79*	7·96	11·
	Female ..	1·17	2·21	4·92	7·34	15·61	15·40	11·34	11·
	Four-eight-tooth—								
	Male ..	1·27	2·69	6·84	10·15	14·34	16·08	13·92	14·
	Female ..	1·02	2·70	4·36	6·60	12·49	16·83	9·41	10·
	Total ..	1·27	2·69	5·99	9·38	15·49	17·06	12·78	13·
Romney Crossbred × Purebred Southdown	Four-eight-tooth—								
	Male, "A" ..	1·62	..	4·95	..	14·99	..	9·56	.
	Male, "B" ..	1·62	..	6·05	..	17·35	..	12·36	.
	Female, "A"	1·22	..	4·78	..	11·45	..	9·56	.
	Female, "B"	1·47	..	4·49	..	16·32	..	9·32	.
	Total ..	1·56	..	5·20	..	16·08	..	10·48	.

* = 15 days.

Although the values of the coefficient of variability show the same general sequence for both breeds they are all distinctly different for each sub-group. Sex and age of ewe may have some effect that is at present obscured. Curves plotted from Hammond's data for Suffolk lambs differ distinctly from those for Southdown and English Leicester lambs. It would be idle to suggest various interactions of environment with heredity which might account for the minor variations occurring, but several general features are worth noting:—

(1) The variability usually increases rapidly after birth, but not always. If some of the ewes with heavy lambs—possibly more common among late lambers—milked well and some of the ewes with light lambs milked poorly this result might not be unexpected. Big lambs would then be relatively heavy at 10 days to 15 days, whereas light lambs would be relatively slow growing if their mothers came on milk tardily.

(2) Decreased variability thereafter is in accordance with the theory that variability decreases with growth-rate. The rate of decrease may vary within fairly wide limits.

(3) The observed variability does not always decrease with age. The Southdowns and English Leicesters appear to have responded differently to circumstances between the ages of 70 days and 130 days.

(4) There is no significant difference in values of coefficient of variability for English and Southdown lambs as a whole.

There is clearly a large amount of variation representing the interaction of the individual at different stages of its life with environment which cannot be attributed to any particular cause. To estimate more accurately the effect of any given variable there would have to be an improved knowledge of the causes underlying this residual variation and their interaction with the variable under consideration.

(10) REDUCTION OF VARIANCE.

In estimating the number of animals necessary to show whether a certain treatment or effect has or has not some real influence on the growth or development of a flock, a knowledge of the variation occurring under standard conditions is most useful. For this purpose the standard deviations given in Table XVI give an indication of the values that may be encountered in a flock at different ages and in different localities.

It will be observed that although the standard deviations and coefficients of variability vary from group to group they resemble each other fairly closely. With this information it is possible to calculate approximately how many lambs would be required to show a given difference or, conversely, how great a difference could be shown by the numbers available.

Using the data given previously (Table XVI) the estimates of Table XVII might be expected under some conditions to be fairly accurate.

TABLE XVII.—ESTIMATES OF MEAN WEIGHTS, STANDARD DEVIATIONS, AND COEFFICIENTS OF VARIABILITY FOR RAM LAMBS (SINGLES) AT DIFFERENT AGES, AND ESTIMATED NUMBERS OF LAMBS REQUIRED TO SHOW VARIOUS PERCENTAGE DIFFERENCES.

Estimates for Ram Lambs.	Age.							
	Birth.		10 Days.		70 Days.		130 Days.	
Mean weight	10 lb.		15 lb.		50 lb.		70 lb.	
Standard deviation ..	1·3		2·6		7·0		10·0	
Coefficient of variability	13 per Cent.		17·3 per Cent.		14 per Cent.		14·3 per Cent.	
Percentage Difference from Mean of Ram Lambs.	Difference in lb.	Number required.	Difference in lb.	Number required.	Difference in lb.	Number required.	Difference in lb.	Number required.
2	0·2	338	0·3	600	1·0	392	1·4	408
4	0·4	85	0·6	150	2·0	98	2·4	102
6	0·6	38	0·9	67	3·0	44	4·2	45
8	0·8	21	1·2	38	4·0	25	5·6	26
10	1·0	14	1·5	24	5·0	16	7·0	16
15	1·5	6	2·3	11	7·5	7	10·5	7
20	2·0	3	3·0	6	10·0	4	14·0	4

These numbers are based on a standard error of the difference, which is just half the difference given.

Supposing that a difference of 6 per cent. in weight of ram and ewe lambs were expected the table shows that thirty-eight lambs of each sex would probably give statistically significant results. On the other hand, if only about twenty of each sex were available, differences of less than 8 per cent. would probably not be satisfactorily established. This example also makes clear a particular use of the coefficient of variability. As it rises in value (as at tailing) the number of animals necessary increases rather rapidly. Its reduction is therefore desirable.

There are so many respects, however, in which lambs within a flock receiving one treatment may differ that the use of groups differing in one respect only is prohibited by their almost inevitably small size. It has been shown by various authors that sex, number of offspring, age of ewe, weight of ewe, time of birth, and various other factors affect the growth of lambs. Some of these have been examined under Canterbury conditions and found to have appreciable effects. The comparison of groups differing in any of these respects must yield misleading results, and frequently obscure real differences which exist, unless their effects are measured and allowed for.

It has been shown above that a large proportion of the total variation which occurs has to be included in the general term of "error variance." The greater the amount of variation which is unaccounted for the greater the size of the flocks necessary in experimental work. Doubtless much variability is genetic in origin. Chapman and Lush(8) found that differences between twins accounted for 44–48 per cent. of the total variation shown by all twin lambs, so that the use of genetically similar sheep would be a considerable advantage if it were possible to get them.

Whilst it seems fairly certain that the technique of weighing, feeding, &c., is responsible for some variation, which is therefore reducible by better methods (Dunlop(7)), the allowance for known variables should be made by methods available now. The reduction in total variance brought about by eliminating two important causes of variation has, in this study of growth-rates in lambs, sometimes reached almost 30 per cent.

ACKNOWLEDGMENTS.

The authors are indebted to Professor R. E. Alexander, Director of Canterbury Agricultural College, for permission to carry out this work, and to Mr. A. Leslie, of the Veterinary Department, for much data and helpful criticism. The records of crossbred sheep have been supplied by Mr. Leslie and were collected with the aid of grants from the Meat Producers Board, Agricultural and Pastoral associations, and other farmers' organizations.

The authors are also indebted to Mr. D. J. Sidey for records of birth-weights of Romney Cross × Southdown lambs in 1932 and 1933.

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THE MILK CONSUMPTION AND GROWTH OF SUCKLING PIGS

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THE lightest pigs at, or before, weaning are by no means always the 'poorest doers' in later life. This fact has been indirectly indicated by many who have worked with the correlations between weights at various ages, and the principle receives practical recognition in the grouping of growing pigs according to size rather than age.

The explanation generally accepted is that there are differences between the quantities of milk produced by sows and between the amounts of milk obtained by individual pigs of a litter. Concerning the differences between sows there can be little doubt [1, 2], but for the differences between the quantities of milk obtained by the pigs of a litter the evidence is mainly indirect. During the progress of research work with a Large White herd in Edinburgh, an effort is being made to isolate genetic differences in the growth-rate of pigs from conception to weaning, and for this purpose it has seemed desirable to obtain some direct evidence on the quantities of milk obtained by suckling pigs. In this way it was hoped to determine whether variations in growth-rate could be completely explained by varying levels in food-supply. In contrast to previous investigations of the milk-production of sows, the work here described involved the weighing of individual pigs before and after suckling instead of litter-weighings. For the immediate purposes of the main investigation it is felt that this particular series of observations has been continued long enough, for although some of the outstanding questions have not yet received an answer, progress must be made in other directions before this can be pursued further.

I. THE METHOD

The method adopted was to remove the pigs from the sow 1½–2 hours before the first weighing and thereafter return them to her for suckling only at 2-hour intervals. The greatest difficulty was found to be the tendency of the pigs to urinate after they had suckled, or even to stop suckling to do so, but this was overcome by turning them out of their bedding and making them stand for some minutes in the dunged area of the pen before weighing. Those which had not urinated could be detected by their almost unchanged weight, and were watched. The error arising from this source is considered negligible. The amount of weight lost by urination varied with the size of the pig from about 10–30 gm. Defaecation caused a very slight loss, usually less than 5 gm. After standing the pigs were weighed to the nearest gram. The technique for obtaining the best weight appears to be to use a direct-reading balance (not a spring one), damp the movement down somewhat, and be prepared to read off the weight quickly. The pigs were then

THE GROWTH-RATE OF LAMBS IN CANTERBURY.

A PRELIMINARY STUDY OF THE VARIATION IN THE GROWTH-RATE OF LAMBS IN CANTERBURY.

By H. P. Donald, M.Agr.Sc., B.Sc., and J. W. McLean, B.Agr.Sc.

Contents.

(1) Summary.

(1) Factors affecting the birth-weight of pure-bred and cross-bred lambs in Canterbury are discussed. It is shown that for the 1933 lambing season purebred Southdown and Romney Cross by Southdown ram lambs were heavier than ewe lambs, whereas purebred English Leicesters did not differ with sex. Two-tooth ewes in general had lighter lambs than older ewes. There is evidence to show that as the lambing season progressed birth-weights increased. The association which existed between birth-weight of lamb and weight of ewe at lambing suggests that these increases are due partly to improved nutrition of the ewes.

The difference in birth-weight between ram and ewe lambs from RX* ewes on light country was found to be negligible if the ewes were lighter than 100 lb. at lambing. It was quite marked when the ewes were 130 lb. or more.

(2) At 70 days old English Leicester ram lambs were still the same weight as the ewe lambs, but the lambs of two-tooth ewes were smaller than those of older ewes. Almost the reverse was true in Southdowns, among which sex, but not age of ewe, had a marked influence on weight. The RX by SD lambs, the males of which had been castrated, did not show any real difference between the sexes.

(3) At 130 days old the weights of English Leicester lambs showed that sex as well as age of ewe was associated with differences in weight, although previously it was not. The Southdown lambs from two-tooth ewes were practically as heavy as those from older ewes, but ram lambs were heavier than ewe lambs.

(4) A correlation was found between the weights at birth and at 70 days which was less than that between the weights at 70 and 130 days old. The birth-weight of the Southdown lambs was a less-reliable indication of their later growth than was the birth-weight of English Leicester lambs.

(5) The variability in weight of lambs at different ages, and its effect on the number of animals required for experimental purposes, is discussed. No serious attempt has been made to place interpretations on the results which have been presented. Such an attempt is considered premature not only because the analysis of variation in growth-rates is far from complete, but because the extent of purely seasonal influences cannot be judged from one year's figures. The necessity in either breeding or experimental work of knowing the nature and importance of the causes of normal variation makes further investigation of them most desirable. The method of analysing variance has been found very useful and its wider use would probably affect considerably the designing of experiments with animals and the value of the results.

(2) INTRODUCTION.

Measurements in any flock reveal in no uncertain way that sheep rarely resemble each other closely in more than a very few respects. This variation may be regarded from some points of view as a disadvantage, but it may be turned to useful account. Apart from being a source of improvements in breeding and management, it provides a subject for study which can yield useful information concerning the growth and production of sheep.

All variations may be related to some antecedent causes. The identification of these causes is necessary to provide a reliable basis for improved breeding and feeding practice, and much agricultural research is designed to achieve this purpose. The mature sheep, however, represents the end product of the reactions of a certain hereditary complex with many environmental influences. If either the inheritance or the environment alters, the end product will be different, and, since it is very unusual for either to be identical for any two sheep, the task of dissociating the various effects is no light one. Any attempt to breed for production or to feed and manage a flock so that the incidence of disease is low and net returns high should include some attack on this task in order to avoid confusion of effects. For instance, it would be inadvisable to judge the genotype of a dairy bull from the records of his daughters unless these had been corrected for age, service period, feeding, and so on. Similarly, growth-rates of lambs not considered in the light of sex, time of birth, or age of ewe would give a misleading indication of the value of a ram for fat-lamb production.

* RX=Romney crossbred; S.D.=Purebred Southdown.

A complete analysis of the relative effects of hereditary and environmental factors is still far from being achieved, but much can be done towards accurate interpretation of observed facts. The application of statistical method to data from experiments with animals undoubtedly sheds more light on their significance, but if the nature and amount of the data to be collected were determined with more reference to their subsequent statistical treatment more information might often be derived from experiments.

Some of the major causes of variation in growth-rate of lambs have been dealt with by Hammond(1). If allowance is made for each of these, there is difficulty in securing, except for rather gross differences, information which is statistically sound from small mobs of sheep. Just how many sheep would be required to show reliably the existence of a difference will depend on the variability due to causes other than those under examination. It is proposed to deal further with this point.

Observations in Canterbury upon a fairly considerable number of ewes and lambs have recently been made to obtain records of performance. These permit an investigation of the degree to which variables such as age and weight of ewe, time of birth, and locality affect the growth, production, and resistance to disease of lambs and ewes. The close connection which has already been found (Leslie(2)) between feeding, production, and diseases of ewes and lambs in Canterbury points strongly to the necessity for keeping records of experimental sheep so that past may assist in explaining present performance. There is therefore probably sufficient justification for the following attempt to estimate the relative effects of certain known factors which modify growth and production. It is hoped also to assist the comparison and selection of rams by the discovery of suitable adjustments to reduce the present difficulty in comparing small progenies.

(3) GENERAL.

Observations have been made on both purebred and crossbred ewe flocks. From approximately 800 Romney cross ewes and their lambs running on light land, performance records for the past two years have been collected for the purpose of research into animal-health problems by the Veterinary Department of Canterbury Agricultural College. Full accounts of the climatic and soil conditions, husbandry practice and methods of experimentation have already been given by Leslie(2, 3), and will not be repeated.

Weighings have been made at birth and three times thereafter of tagged lambs in purebred English Leicester and Southdown flocks. These sheep were subjected to practically the same climatic conditions as the crossbreds, but obtained better feed. They are run on medium to heavy land and receive a comparative abundance of feed at all times. Although the sire is known for the majority of lambs, it has not been considered desirable to present the inconclusive data which can be derived from one year's records. Discussion of variation in twins will also be excluded from this paper.

The English Leicester flock has been inbred fairly intensively for the past fifteen years. During this time only three sires, already related to the flock, have been introduced. This is not true to nearly the same extent in the Southdowns.

Shearing took place in the third week of November, and weaning in the third week of January for both the purebred and crossbred flocks. At tailing, the ram lambs in the purebred flocks were not castrated.

(4) CLIMATIC AND FEED CONDITIONS DURING THE YEAR (1933–34).

The winter of 1933 was not particularly severe but partial failure of the turnip crop necessitated dry feeding with chaff and hay in addition to rationed turnip tops for the crossbred ewes until well into lambing. During the latter half of lambing the growth of grass improved and the later ewes lambed in better condition. All ewes were put on to green-feed oats after lambing. As grass became available they were shifted from the oats. The purebreds received grass supplemented with mangels, hay, chaff, and molasses. They lambed on good grass and continued thereon until the last weighing dealt with in this paper. The lambing season was popularly regarded as a good one. Weather conditions were at no time very severe.

The last ten days of August were for the most part overcast, but, except for four rainy spells, September was fine and mild. No very cold nights were experienced during the whole lambing season.

About the beginning of November continued dry weather caused a shortage of grass on light country, and ewes and lambs suffered a check. There is no evidence that this occurred on heavier land to any appreciable extent.

(5) VARIATION IN BIRTH-WEIGHTS.

(*a*) *Technique.*—All lambs were weighed and tagged as soon as possible after birth. With large flocks it is not practicable to handle all lambs at any constant interval after birth, so that two sources of error are introduced. For some time the lambs are wet with amniotic fluid, and gradually lose weight as it dries. Any suckling of the ewe before weighing will counteract and possibly outweigh this loss. If ten to twenty-four hours elapse before weighing there is an appreciable error introduced by the amount of milk obtained by the lamb. Weighings at short intervals after birth have shown that there is usually a slight decrease in weight, followed by an increase of anything up to 1 lb. at the end of twenty-four hours. This agrees with the experience of Sidey (4).

The field practice followed was to weigh lambs throughout the day. Since most of the lambs are dropped during the night they would be from three to twelve hours old before weighing. Consequently mean birth-weights are possibly slightly higher than the real "dry weight at birth."

Further, the recording of weights to the nearest tenth of a pound, as was done, does not necessarily indicate considerable accuracy in measuring the birth-weights. It may well be assumed that for a reasonably large number of lambs any discrepancy would be practically the same for different groups and that comparisons between them on a basis of observed weights would be valid. This assumption, however, may not be justified, since Romney cross ewes have been found with lambs which at twenty-four hours old were the same weight as at birth. This may be due to failure of the lambs to suckle,

but, if it could be attributed in part at least to failure of the ewe to milk well immediately after parturition, then such a characteristic for a strain or flock as a whole is conceivable—*e.g.*, for Southdowns, or for poorly nourished two-tooth ewes. Birth-weights would then be biased in favour of better milking-ewes.

Richter and Brauer, quoted by Hammond (*loc. cit.*) found that lambs took on the average 1·7 days to regain the weight lost after birth from evaporation of moisture. This is considerably in excess of the time required by the lambs examined in Canterbury.

(*b*) *Effect of Season.*—Since it has been shown that the birth-weight of lambs may be modified by the condition of the ewe at lambing, mean birth-weights might be expected to vary from season to season. The influence of different planes of nutrition, however, need not necessarily have the same effect. Breeds differ in ability to adjust themselves to a shortage of feed, and individual ewes existing on a diet deficient in any way may not sacrifice themselves equally for the sake of their lambs. Seasonal changes may therefore be reflected to different extents in the birth-weight of lambs.

Table 1 shows the mean birth-weights of single lambs obtained in Canterbury during the last two years.

TABLE 1.—MEAN BIRTH-WEIGHT OF SINGLE LAMBS (BOTH SEXES) FOR 1932 AND 1933.

Breed.		Year.	Mean Birth-weight.	No.	Remarks.
Ewe.	Ram.				
			A. For Light Land.		
			lb.		
RX	SD	1932	9·78	571	Wintered on turnips and chaff.
RX	SD	1933	9·34	405	Shortage of turnips in winter.
			B. For Medium and Heavy Land.		
RX	SD	1932	10·18	74	
RX	SD	1933	9·43	51	
EL	EL	1933	9·84	70	Well wintered.
SD	SD	1933	8·22	65	Well wintered.
R	R	1933	10·02	31	Well wintered.

EL = Purebred English Leicester; R = Purebred Romney; SD = Purebred Southdown; RX = Crossbred Romney.

There is some evidence of a seasonal influence which is probably related to the winter feed available. It is noticeable for the RX × SD lambs on light country and for similar lambs on heavy country for 1932–33. Hammond has found a seasonal variation over a much longer period of years which he attributes mainly to an influence of rainfall on available feed. A comparison between the mean birth-weights of the comparable lambs (RX × SD) shows slightly heavier weights for the lambs raised on the better land. This difference is probably due to the same cause as operates from season to season.

The value of these figures is strictly limited because they represent only the relation between general husbandry conditions and birth-weight, and for most purposes, experimental or otherwise, this is insufficient. The explanation of the seasonal and local variation must be sought from a more detailed study.

Inset—Growth-rate of Lambs.

Such detailed studies have been facilitated in recent years by the introduction of statistical method designed to extract the maximum amount of information from observed data. The analysis of variance as developed by Fisher(5) has proved very useful. Examples illustrating its use have been published by Fisher (*loc. cit.*), Yates(6), and Dunlop(7).

(*c*) *Factors affecting Birth-weight.*—The following factors which are known to influence birth-weight will be examined in their relation to Canterbury conditions: Sex of lamb; age of ewe; time of birth; weight of ewe; winter feeding.

Sex of Lamb and Age of Ewe.—It is common knowledge that ram or wether lambs have a higher average weight than ewe lambs, and that two-tooth ewes as a rule do not produce such well-grown lambs as older ewes. The magnitude of these differences for the 1933 season is shown in the following analysis of the variance occurring in two flocks of purebred ewes. In these analyses it will be noted that all single lambs from each flock have been used to obtain an estimate of the proportions which variation in birth-weight due to sex bears to variation caused by age of ewe within each sex group, and to residual variation. This latter is a measure of the variation due to all causes not specified—*i.e.*, heredity, weight of ewe, accidents, &c.

TABLE II.—COMPARISON OF VARIANCE DUE TO SEX OF LAMB AND AGE OF EWE WITH THAT DUE TO ALL OTHER CAUSES.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOG_e	*z*	P
			Southdown Lambs.					
Males ..	7·74 (7)	8·88 (24)	Sex ..	1	9·44	1·123	0·965	0·01
Females	7·50 (16)	8·17 (18)	Age of ewe	1	10·76	1·188	1·030	<0·01
Mean ..	7·57 (23)	8·57 (42)	Error ..	62	1·37	0·158	..	..
			Total ..	64	1·64	..	..	..
			English Leicester Lambs.					
Males ..	9·16 (11)	10·31 (27)	Sex ..	1	1·49	0·199	0·040	..
Females	9·10 (14)	10·13 (18)	Ewe's age	1	18·31	1·454	1·295	<0·01
Mean ..	9·12 (25)	10·24 (45)	Error ..	67	1·38	0·159	..	..
			Total ..	69	1·62	..	..	..

NOTE.—The total variance, which is obtained by adding the squares of the differences of each lamb-weight from the mean weight of all lambs, is divisible into portions attributable to sex of lamb, age of ewe, random error, &c. These portions when divided by the corresponding degrees of freedom (D.F.) give the figures in the column headed "mean square." These mean squares are compared with the aid of the *z* transformation. Half the natural logarithm of each mean square is calculated, and the value of *z* is found by difference. To compare, for example, the variance due to sex of lamb with that due to random error in birth-weight of Southdown lambs, *z* is obtained from the values of ½ LOG_e (1·123–0·158) = 0·965. The probability (P) that this value could arise by chance is found from Fisher's table of *z*. If P is less than 5 per cent. (0·05)—that is, if the chances are more than 20 to 1 against this value of *z* being a purely accidental one, the difference in observed weights is regarded as significant.
The numbers of lambs from which the mean weights were calculated are shown in brackets.

According to the table of *z* the chances are about 100:1 that the difference in mean birth-weights of ram and ewe lambs in the Southdown flock is a real one. This is in accordance with the usual belief. In the English Leicester flock, however, the variance due to sex (1·49) is very little greater than that due to random variance (1·38) and, on this evidence, there are no grounds for concluding that there is any difference between the sexes in weight at birth. In both flocks the age of the ewe is responsible for a greater variance than sex.

In the English Leicester flock about 14 per cent. of the variance may be attributed to age of ewe, while in the Southdowns the corresponding figure is about 9 per cent. The error-variance has been reduced to 85 per cent. of the total variance in both flocks by eliminating sex and age of ewe. It may be noted here that the lambs of two-tooth ewes differ less in weight with sex than those of older ewes.

Although there is evidence to show that birth-weight may increase with successive lambs at least until the ewe is full-mouthed the only distinction which has been made above is that between two-tooths and older ewes. It is probable, however, that further analysis would reduce the error-variance still more.

Sex of Lamb and Winter Feeding.—Much the same conclusion regarding the effect of sex can be drawn from the following table showing a similar analysis of variance for lambs from Romney Cross ewes on light land.

Although these ewes have been fed in two different ways during winter the variance due to sex is comparable with the error-variance as before. Treatment has been eliminated in place of age of ewe. As no two-tooth ewes were present the comparison of sex and error-variances for the different localities is regarded as valid for the feeding and husbandry practices concerned.

TABLE III.

Lambs.	Treatment "A."	Treatment "B."	Variance.	D.F.	Mean SQ	½ LOG_e	*z*	P
Males ..	10·81 (39)	9·36 (52)	Sex ..	1	12·75	1·273	0·906	>0·01
Females	9·80 (65)	9·00 (44)	Treatment	1	64·15	2·081	1·714	<0·01
			Error ..	197	2·08	0·367	..	..
			Total ..	199	2·45	..	..	..

The odds that there is an effect of sex over the whole flock are a little lower than 100 : 1. If the effect of sex had been calculated on the treatment groups separately it would have been much greater. The considerable difference between males and females in the group getting treatment "A" has been somewhat reduced by combining them with those receiving treatment "B."

Unless the groups under treatments "A" and "B" differed in respect of any other factors affecting birth-weight, there must have been interactions between treatment and birth-weight which were different in the groups. In these groups the total variance has been reduced by about 3 per cent. by eliminating variance due to sex.

Time of Birth.—Hammond gives figures for three seasons showing that early lambs (singles) were about 2·2 lb. lighter at one week old than late lambs. To a certain extent this association of time of birth and weight has been found in Canterbury in 1932 and 1933. Mean birth-weights of English Leicester lambs, divided into three

groups according to time of birth, showed significant differences. The estimation of variance due to this cause resulted in a further reduction of error-variance from 1·38 to 1·25.

Weight of Ewe.—Whilst the association between weight at birth and time of birth may be accepted, the underlying causes of this are not apparent from lamb-weights alone. It has been suggested that the condition of the ewe improves as the spring grass becomes available, and that the lamb benefits as a result. An investigation of this point is possible if the weights of ewes at lambing are known.

The weighing of many ewes just before or after each lambs is impracticable. It is possible, however, to weigh all ewes just before lambing commences, and then to weigh unlambed ewes at some time during the lambing season. This was done in the flock of RX ewes. From these two weighings the increase in weight could be calculated. This was found to be practically the same for ewes of all weights. The actual weight of ewes at lambing was then calculated from the live weight increase per day so determined, the date of lambing, and its weight at the last weighing, and includes the weight of the lamb.

Although the weights of individual ewes increased as lambing proceeded, it does not follow that the mean weights of ewes lambing during successive periods should show a progressive increase. During the 1933 lambing season the mean weights shown in Table IV of ewes at lambing were calculated by the above method.

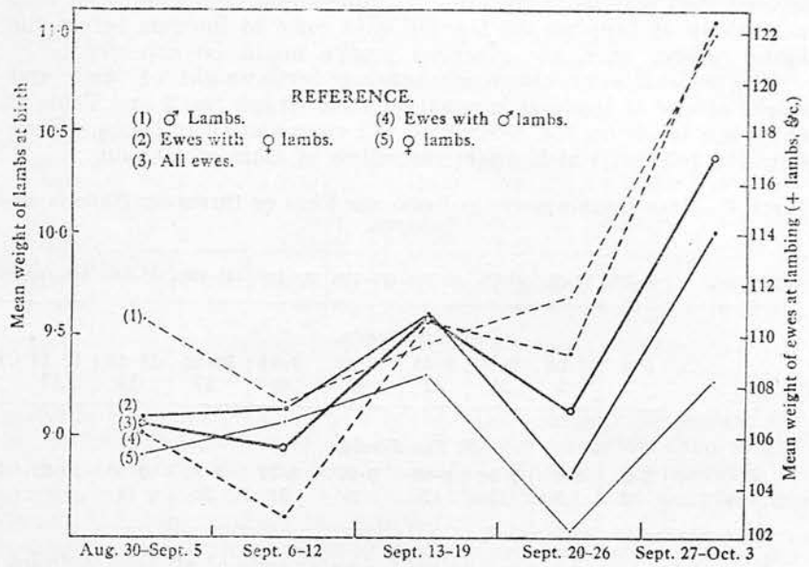
TABLE IV.—MEAN WEIGHTS OF EWES AND LAMBS AT LAMBING FOR WEEKLY PERIODS.

——	First Period.	Second Period.	Third Period.	Fourth Period.	Fifth Period.
Weight of ewes with male lambs	106·0 (59)	102·8 (30)	110·7 (65)	109·3 (20)	122·4 (17)
Birth-weight of male lambs	9·59 (59)	9·17 (30)	9·48 (65)	9·71 (20)	11·01 (17)
Weight of ewes with female lambs	106·9 (54)	107·2 (47)	110·9 (66)	104·4 (18)	114·1 (29)
Birth-weight of female lambs	8·92 (54)	9·07 (47)	9·31 (66)	8·54 (18)	9·28 (29)
Mean weight, all ewes ..	106·4	105·5	110·8	107·0	117·1
Mean weight, all lambs ..	9·27	9·07	9·39	9·16	9·92

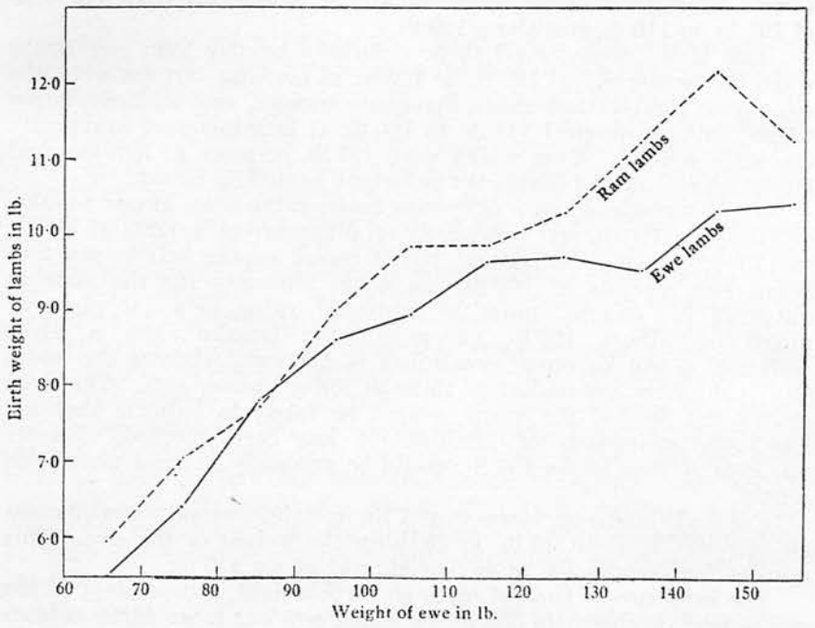
First period, 30th August to 5th September; second period, 5th to 12th September; third period, 13th to 19th September; fourth period, 20th to 26th September; fifth period, 27th September to 3rd October.

It will be noted that there is a slight drop from the first period to the second, and a much larger one from the third to the fourth. This is also shown in Graph No. 1. Consequently, if there is a close connection between birth-weight of lamb and weight of ewe, a continuous increase in birth-weight of lambs could not be expected with the passage of time.

Just why the mean weight of ewes should not show a regular increase corresponding to that of any one ewe is doubtful. A possible explanation is suggested by the fact that the two decreases in weight are separated by a period approximately equal to that



GRAPH NO. 1.—The mean weights of ewes and lambs at lambing for weekly periods.



GRAPH NO. 2.—The mean birth-weights of lambs for ewes of different weights at lambing.

between heat periods in the ewe. If under light land conditions with no flushing at tupping the heavier ewes come to the ram before the lighter poorer ones, the observed results might be expected.

The general correspondence between birth-weight of lamb and weight of ewe at lambing is apparent from Graph No. 2 and Table V which are based on the records of 432 ewes and their lambs. They show the relation which exists regardless of time of lambing.

TABLE V.—MEAN BIRTH-WEIGHTS OF LAMBS FOR EWES OF DIFFERENT WEIGHTS AT LAMBING.

Ewe-weight (lb.).	61–70.	71–80.	81–90.	91–100.	101–110.	111–120.	121–130.	131–140.	141–150.	151–1
A. Ram Lambs.										
Mean	5·9	7·08	7·74	9·05	9·85	9·84	10·32	11·25	12·18	11·3
Number	1	4	21	42	46	45	17	13	12	1
B. Ewe Lambs.										
Mean	5·5	6·4	7·86	8·66	8·99	9·72	9·76	9·55	10·3	10·4
Number	2	3	22	47	53	51	29	13	9	1

Except for thirty-eight English Leicester ewes of all ages included to show the relation at low ewe-weights, the ewes are four-, six-, and eight-tooth Romney Cross. It is apparent that heavy ewes give birth as a rule to heavy lambs. While this may apply to both male and female lambs, it does not apply equally to both sexes at ewe-weights of 101 lb. to 110 lb. and above 120 lb.

Ram lambs were found to be definitely heavier than ewe lambs when the ewes weighed 100 lb. to 110 lb. at lambing, but not when the ewes were lighter than this. Strangely enough, ram and ewe lambs whose mothers weighed 111 lb. to 120 lb. at lambing were practically the same weight. Ewes which were 131 lb. or more at lambing had lambs which differed distinctly in weight according to sex.

Why there should be a difference between the sexes at ewe weights of 100 lb. to 110 lb. and practically no difference at weights of 110 lb. to 120 lb. cannot be explained, but it would appear safe to say that below ewe weights of 100 lb. the usual tendency for the male to outweigh the female cannot be expressed owing to a low plane of nutrition. Above 120 lb. ewe-weight the females show a slight response to the improved conditions in the ewe, whereas the males still show increases similar to those at lower ewe-weights. The drop at the tail end of the graph cannot be taken to indicate that the maximum expression of birth-weight has been reached. Larger numbers of ewes above 150 lb. would be necessary to show where this occurs.

For male lambs an increase of 1 lb. in weight usually accompanies an increase of about 10 lb. to 15 lb. in the weight of the ewe. This applies for females up to ewe-weights of about 115 lb.

The influence of time of birth on birth-weight, independent of the ewe-weight, is shown in Table VI which sets out mean birth-weights of lambs from ewes of the same weight at lambing in the five periods into which the lambing period was divided.

TABLE VI.—MEAN BIRTH-WEIGHTS OF LAMBS FROM EWES OF EQUAL WEIGHT AT LAMBING.

—	30th August to 5th September.	6th to 12th September.	13th to 19th September.	20th to 26th September.	27th September to 3rd October.
Ewes 105–110 lb.—					
Males	9·67 (7)	9·60 (3)	9·25 (13)	8·73 (3)	11·65 (2)
Females	8·59 (7)	8·73 (9)	8·97 (10)	9·56 (5)	9·82 (5)
Ewes 111–115 lb.—					
Males	9·78 (9)	9·45 (4)	9·57 (6)	10·33 (3)	11·17 (3)
Females	9·94 (9)	9·80 (7)	9·96 (7)	..	9·35 (2)
Ewes 105–115 lb.—					
Males	9·73 (16)	9·51 (7)	9·35 (19)	9·53 (6)	11·36 (5)
Females	9·35 (16)	9·20 (16)	9·38 (17)	9·56 (5)	9·69 (7)
All lambs	9·54 (32)	9·30 (23)	9·36 (36)	9·55 (11)	10·38 (12)

With the possible exception of the last period, the means for the various periods do not show any greater variation than might be expected with the numbers available. Much of the increase in birth-weight which takes place as lambing passes may therefore be attributed to improved condition of the ewe.

The possibility that weight of the ewe influences the birth-weight of the lamb to an extent which is modified by the age of the ewe has not yet been investigated.

(6) VARIATION IN WEIGHTS AT DIFFERENT TIMES UP TO WEANING.

In order to place all lambs on a comparable basis subsequent to birth it has been found necessary to calculate the weight at definite ages from observed weights. Since most weights are recorded on particular days the actual ages of the lambs vary and the weights are not comparable. The probable weights at a given age—*e.g.*, 10, 15, 70, or 130 days—have therefore been calculated by adding to or subtracting from the observed weight an amount equal to the live-weight increase per day, shown up to day of weighing times the number of days short of or in excess of the required age. This would be quite sound only if the average live-weight increase per day used were a true indication of the growth-rate between the actual age at weighing and the standard age. Growth-curves for lambs weighed at short intervals (10 days) show that the live-weight increase per day is practically constant at least up to 70 days, provided the feed-supply is adequate. So far, then, as calculated weights at 10, 15, and 70 days are concerned, the error introduced would be small. In any case, the growth-rate will not alter greatly during the few days by which most lambs differ from the standard, and the error, therefore, will be correspondingly small. For each standard age the weight was calculated from the growth-rate between the weighing at this time and the previous one. All calculations which follow have been based only on healthy lambs.

(*a*) *Weight at Tailing-time.*—Most English Leicester lambs were tailed at about 10 days old and the Southdown lambs at about 15 days. The following mean weights and variances were obtained.

TABLE VII.—MEAN WEIGHTS AND VARIANCE AT TEN DAYS FOR ENGLISH LEICESTER LAMBS, AND AT FIFTEEN DAYS FOR SOUTHDOWN LAMBS.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOG_e	z	P
			A. English Leicester Lambs.					
Males ..	15·32 (10)	17·37 (27)	Sex ..	1	24·10	1·59	0·76	<0·05
Females	14·29 (14)	16·68 (18)	Age of ewe	1	76·03	2·17	1·34	<0·01
Mean ..	14·72 (24)	17·10 (45)	Error ..	66	5·21	0·83	..	..
			Total ..	68	5·53	..	..	..
			B. Southdown Lambs.					
Males ..	15·27 (6)	16·74 (23)	Sex ..	1	22·54	1·56	0·61	>0·05
Females	14·34 (16)	16·04 (18)	Age of ewe	1	34·88	1·78	0·83	<0·05
Mean ..	14·59 (22)	16·43 (41)	Error ..	60	6·66	0·95	..	..
			Total ..	62	7·37	..	..	..

It will be noted that about 20 per cent. of the total variance in English Leicester flock at this age may be attributed to differences in sex of lamb and age of ewe, whereas the corresponding figure for the Southdowns is 10 per cent.

It is clear that both ram and ewe lambs from two-tooth ewes are lighter than those from older ewes, just as they were at birth. At 10 days, however, the English Leicester ram lambs appear to have exceeded the ewe lambs in weight, although they were equal at birth. On the other hand, the difference in weight between the sexes among Southdown lambs is not as marked at 15 days as at birth. There would appear to be less than twenty chances to one that the difference shown by the means is not a chance one. In view of the difference which will be established between the sexes at 70 days old, it would be safer to suppose that the apparently slighter effect of sex at 15 days is an outcome of the increased variance due to a variety of causes such as content of stomach, different growth-rates, &c.

(*b*) *Weight at 70 Days.*—This corresponds approximately to weight at shearing-time.

TABLE VIII.—MEAN WEIGHTS AND VARIANCE AT SEVENTY DAYS FOR ENGLISH LEICESTER LAMBS.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOG_e	z	P
Males ..	46·38 (10)	53·38 (25)	Sex ..	1	114·17	2·37	0·49	>0·05
Females	46·34 (13)	50·48 (18)	Age of ewe	1	479·70	3·09	1·21	<0·01
Mean ..	46·36 (23)	52·17 (43)	Error ..	63	42·54	1·87	..	..
			Total ..	65	50·37	..	..	..

The observed value of $z = 0·49$, is less than the value of 0·69 demanded for P = 0·05, and the effect of sex cannot be regarded as

significant. The difference of 2·9 lb. between male and female lambs of older ewes taken separately is not significant.

Mean weight of males 53·38 ± 1·38
50·48 ± 1·49
Difference 2·90 ± 2·03

The difference is not much greater than its standard error.

A comparison of the error-variance shown in Table XII with that found by calculating the weight at standard age (70 days) using a correction for lambs older than 70 days based on the growth-rate from shearing till weaning time showed no significant difference.

	Mean SQ.	LOG_e.	1/n.
Error variance (Table XII) ..	42·54	3·75	0·01587
Error variance (Alternative Method)	41·69	3·73	0·01587
Difference	..	0·02	..
	z =	0·01	

Variance of $z = 0·01587$
SD of z $= 0·126$

The comparable figures for the Southdown flock are as follows:—

TABLE IX.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOG_e	z	P
Males ..	48·40 (6)	49·17 (23)	Sex ..	1	249·56	2·76	1·03	<0·01
Females	43·39 (15)	46·38 (16)	Age of ewe	1	72·28	2·14	0·41	>0·05
Mean ..	44·82 (21)	48·03 (39)	Error ..	57	32·16	1·74	..	..
			Total ..	59	36·52	..	..	..

Among the Southdowns the effect of sex has again become pronounced. Taking males and females separately the age of ewe does not affect the weight of either much more than undetermined causes. Taking males and females together, however, the chances are slightly more than 20 : 1 that the lambs of two-tooths are lighter than those of older ewes.

Under light land conditions the flock which has been considered showed no appreciable difference due to sex. This is shown below.

TABLE X.

Lambs.	Treatment "A."	Treatment "B."	Variance.	D.F.	Mean SQ.	½ LOG_e	z	P
Males ..	51·46 (24)	48·96 (27)	Sex ..	1	23·81	1·59	−0·05	..
Females	49·95 (41)	48·19 (28)	Treatment	1	125·43	2·42	0·78	<0·05
Mean ..	50·51 (65)	48·57 (55)	Error ..	117	26·47	1·64	..	..
			Total ..	119	27·28	..	..	..

The chances are, therefore, that treatment "A" resulted in a superiority of both male and female lambs over those under treatment "B."

(c) *Weight at 130 Days.*—This corresponds to weight at weaning. Between the ages of 70 and 130 days the RX × SD lambs on light land suffered a shortage of feed. The growth-rates fluctuated widely according to the age of the lamb, and the weights at 130 days, which would have little value in this connection, have not been calculated. The purebred lambs went on to weaning-time with a good supply of feed, and the following means and variances were obtained.

TABLE XI.—MEAN WEIGHTS AND VARIANCE AT 130 DAYS FOR ENGLISH LEICESTER LAMBS.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOGe	z	P
Males ..	67·70 (10)	80·49 (25)	Sex ..	1	805·29	3·35	1·16	<0·01
Females	66·46 (13)	72·27 (18)	Age of ewe	1	1422·99	3·63	1·44	<0·01
Mean ..	67·00 (23)	77·05 (43)	Error ..	63	79·22	2·19	..	..
			Total ..	65	111·06	..	..	..

At this age both sex and age of ewe effects are very marked taking the flock as a whole. It is apparent, however, that the sex-variance is mostly due to the superiority in weight of the ram lambs of older ewes. The elimination of variance due to both these factors has reduced the error variance to about 71 per cent. of the total variance.

It will be remembered that there was no definite evidence of any difference between the sexes at birth for either class of ewe among English Leicesters, although perhaps such a difference was foreshadowed by a slight apparent difference in the means at birth and at 70 days. The ram lambs of two-tooth ewes are still very little different from the ewe lambs. Whether this is due to the inability of two-tooth ewes to maintain a sufficient milk-supply to allow their ram lambs to show any faster growth than ewe lambs, or whether the effects of poorer nutrition in utero are responsible, is not apparent from the data. The number of two-tooth ewes with lambs does not permit of an investigation of the possibility that the lambs which are born as heavy as those of older ewes show differences in growth-rate according to sex, provided that milk-supply does not inhibit such a tendency.

That the results are not true for all two-tooth ewes is shown by the figures for the Southdown lambs.

TABLE XII.—MEAN WEIGHTS AND VARIANCE OF SOUTHDOWN LAMBS AT 130 DAYS OLD.

Lambs.	Two-tooth Ewes.	Older Ewes.	Variance.	D.F.	Mean SQ.	½ LOGe	z	P
Males ..	71·10 (6)	72·19 (22)	Sex ..	1	1005·45	3·46	1·30	<0·01
Females	62·64 (15)	64·59 (16)	Age of ewe	1	45·35	1·91	..	..
Mean ..	65·06 (21)	68·99 (38)	Error ..	56	73·95	2·15	..	..
			Total ..	58	89·52	..	..	..

It has therefore been no disadvantage to these Southdown lambs to be the offspring of two-tooth ewes. The difference between the sexes is most marked. The results in both these respects were quite different in the English Leicester flock.

At birth Southdown lambs showed differences in weight depending on their sex and on the age of their dams. At 70 days sex-differences were still marked, but those due to age of ewe had diminished to non-significance. At 130 days the variance due to this cause was less than that due to "random error."

(7) GROWTH-RATES.

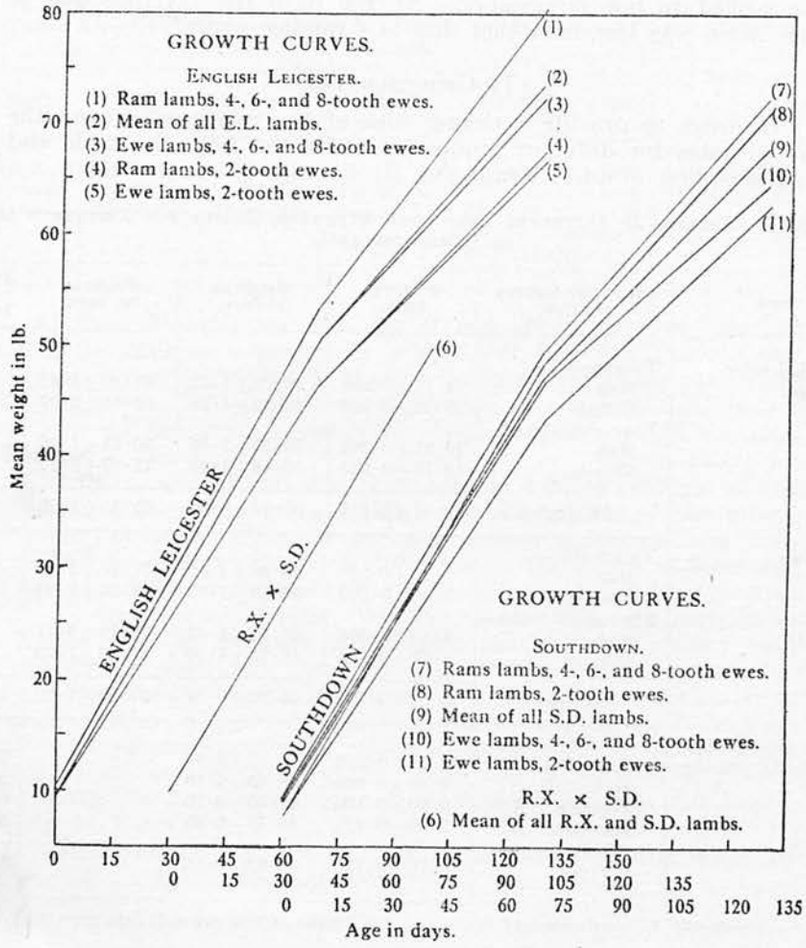
In order to provide a clearer idea of the relations between the growth-rates for different groups of lambs, the following table and corresponding graphs (Graph No. 3) have been constructed.

TABLE XIII.—WEIGHTS AT DIFFERENT AGES WITH STANDARD ERRORS FOR DIFFERENT GROUPS OF LAMBS (SINGLES).

Breed.	Age of Ewe, and Sex of Lamb.	Weight at Birth.	Weight at 70 Days.	Weight at 130 Days.	Number of Lambs.
English Leicester ..	Two-tooth—				
	Male ..	9·16±0·285	46·38±1·52	67·70±1·82	10
	Female ..	9·10±0·259	46·34±1·78	66·46±2·07	13
	Four–eight-tooth—				
	Male ..	10·31±0·261	53·38±1·38	80·49±1·96	25
	Female ..	10·13±0·245	50·48±1·49	72·27±2·17	18
	All singles ..	9·84±0·151	50·14±0·87	73·55±1·29	66
Southdown ..	Two-tooth—				
	Male ..	7·74±0·338	48·40±1·57	71·10±3·21	6
	Female ..	7·50±0·293	43·39±1·27	62·64±1·90	15
	Four–eight-tooth—				
	Male ..	8·88±0·264	49·17±1·43	72·19±2·17	22
	Female ..	8·17±0·240	46·38±1·09	64·59±1·65	16
	All singles ..	8·22±0·160	46·91±0·77	67·59±1·22	59
Romney Crossbred × Purebred Southdown	Four–eight-tooth—				
	Males "A"* ..	10·81±0·259	51·46±1·03	..	39 24†
	Males "B" ..	9·36±0·225	48·96±1·16	..	52 27
	Females, "A"	9·80±0·139	49·95±0·75	..	65 41
	Females, "B"	9·00±0·221	48·19±0·85	..	44 28
	Total ..	9·70±0·110	49·62±0·48	..	200 120

* = Treatment "A" and Treatment "B." † = Number at birth and at 70 days respectively.

Bearing in mind the numbers of lambs used in calculating these means the most striking feature of Graph No. 3 is the close agreement in live-weight increase of all lambs up to 70 days. Even on light land the lambs have grown practically as fast as those on heavier land. The crossbred nature of the lambs may be involved. Also under similar conditions the English Leicester lambs have grown a very little faster than the Southdowns. Whether Southdowns of equal birth-weight to English Leicester would preserve this relation has yet to be discovered.



GRAPH NO. 3.—Growth curves of lambs of different breeds.

From 70 to 130 days the English Leicesters show, on the whole, a smaller decrease in growth-rate than the Southdowns. The relation between the various mean growth-rates calculated from Table XIII is shown below.

TABLE XIV.—MEAN GROWTH-RATES PER DAY.

Breed.	Age of Ewe and Sex of Lamb.	Growth-rate, Birth–70 Days.	Growth-rate, 70–120 Days.	Ratio.
English Leicester	Two-tooth—	lb.	lb.	
	Male ..	0·53	0·36	1·47
	Female ..	0·53	0·34	1·56
	Four–eight-tooth—			
	Male ..	0·62	0·45	1·38
	Female ..	0·58	0·36	1·61
	Total, all lambs	0·58	0·39	1·49
Southdown	Two-tooth—			
	Male ..	0·58	0·38	1·53
	Female ..	0·51	0·32	1·59
	Four–eight-tooth—			
	Male ..	0·58	0·38	1·53
	Female ..	0·55	0·30	1·83
	Total, all lambs	0·52	0·35	1·49
Romney Crossbred × Purebred Southdown	Four–eight-tooth—			
	Male ..	0·57	..	..
	Female ..	0·57	..	..
	Total, all lambs	0·57	..	..

(8) RELATION BETWEEN WEIGHTS OF LAMBS AT DIFFERENT AGES.

It will have been noted from the growth curves just examined that, as a rule, those groups of lambs (within a breed) which had a comparatively low mean birth-weight showed relatively low mean-weights at subsequent weighings. There is no measure provided by Table XIII of the degree to which this is true of any one lamb. The importance of knowing at what age lambs may be safely selected for breeding-purposes on a growth-rate basis has been pointed out by Hammond. For experimental work designed to test the effect of a treatment on growth-rate, it is obviously also important. Study of individual records shows that a lamb, which is heavier than another at any one age, is not necessarily heavier than the other when they are older. This is particularly true of young lambs. The chances of malnutrition, disease, or accidents impeding growth are probably greater at this age than they are subsequently. It might be suggested also that birth-weight may be less dependent on the hereditary "growth force" or efficiency in converting environment into body substance than later weights.

Certain correlations which existed between the weights of lambs at birth and at 70 days, and between weights at 70 and 130 days are appended below (Table XV).

TABLE XV.

Group.	*r* for Weights at Birth and 70 Days.	Number of Lambs.	P	*r* for Weights at 70 and 130 Days.	Number of Lambs.	P
English Leicester—						
Ram lambs, 2-tooth ewes ..	0·675	10	<0·04	0·770	10	<0·01
Ewe lambs, 2-tooth ewes ..	0·495	13	<0·1	0·703	13	<0·01
Ram lambs, 4–8-tooth ewes	0·770	25	<0·01	0·908	25	<0·01
Ewe lambs, 4–8-tooth ewes	0·636	18	<0·01	0·762	18	<0·01
Combined	0·681	66	<0·01	0·831	66	<0·01
Southdown—						
Ram lambs, 2-tooth ewes	..	..	..	..	..	..
Ewe lambs, 2-tooth ewes ..	0·486	15	<0·1	0·807	15	<0·01
Ram lambs, 4–8-tooth ewes	0·396	23	0·05	0·936	22	<0·01
Ewe lambs, 4–8-tooth ewes	0·336	16	>0·1	0·891	16	<0·01
Combined	0·40	54	<0·01	0·898	53	<0·01
Romney Crossbred × Purebred Southdown—						
Wether lambs	..	..	..	..	..	..
Treatment "A".. ..	0·768	23	<0·01	..	..	..
Treatment "B".. ..	0·577	27	<0·01	..	..	..
Ewe lambs, "A" ..	0·544	41	<0·01	..	..	..
Ewe lambs, "B" ..	0·766	28	<0·01	..	..	..
Combined	0·662	119	<0·01	..	..	..

Apart from the value of 0·495 for ewe lambs of two-tooth ewes the correlations between birth-weight and weight at 70 days among all English Leicester lambs seem fairly similar. However, the value of 0·495 is quite within the range of a normal deviate (for those lambs) from a general value of $r = 0·7$. The corresponding values for Southdown lambs are lower, and practically significantly different.

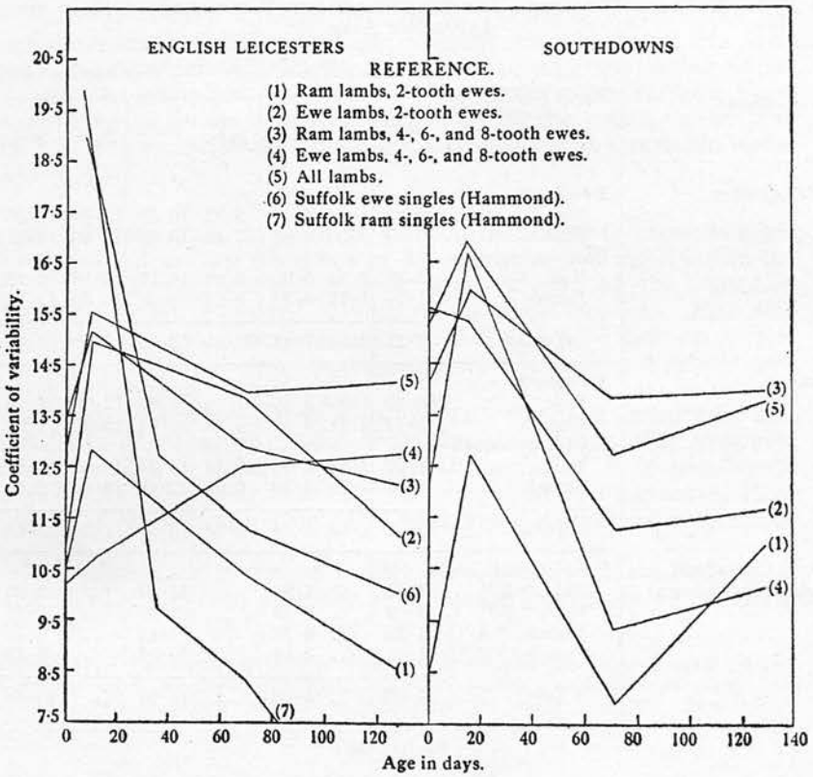
	r	*z*	1/n–3.
English Leicester lambs	= 0·681	0·831	0·0222
Southdown lambs ..	= 0·40	0·429	0·0185
Difference ..	= ..	0·402 ±	0·202

The difference in value of z is almost twice the standard error, and there is a strong possibility that there was a real difference in the correlations exhibited by the two breeds. The close resemblance of the correlations for both breeds of the weight at 70 days with that at 130 days would indicate that the causes of the apparently low previous correlation in Southdowns have been removed. If recorded birth-weight were for some reason not a good indication of the growth-force, or if the environment—*e.g.*, milk-supply—did not act equally on lambs of the various weight classes, this result might be understandable.

A comparison of the values of r for crossbred and purebred lambs is interesting. The factors affecting the growth of these crossbred-lambs, although probably different in some respects from those acting on the purebred lambs, appear to have had their effects distributed in much the same way as in the English Leicester flock.

For either Southdown or English Leicester lambs it may be assumed that weight at 70 days provides a fairly reliable indication

of growth up to 130 days if the supply of feed, &c., is not greatly different from that in the summer of 1933–34. It may be concluded also that birth-weight is correlated with subsequent growth. The value of the correlation may, however, vary according to breed and other circumstances. Hammond, for example, gives a value of $r = 0·528 \pm 0·088$ for the correlation between weight at one week old and weight at twenty weeks for Suffolk ewe lambs.



GRAPH NO. 4.—The coefficients of variability of mean weights of lambs at different ages.

(9) VARIABILITY IN WEIGHT AT DIFFERENT AGES.

Relative variability as measured by the coefficient of variability does not remain constant during growth. It follows that the response of individuals within a flock to the stimulus of environment does not vary directly as their weight. In other words, if the coefficient of variability increases, light lambs become lighter and heavier ones heavier than they would if the coefficient of variability remained the same. If the coefficient of variability decreases, then for some reason the light ones have caught up somewhat in proportion to their size on the heavy ones. Hammond (*l.c.*), who found that the coefficient of variability decreased with age, subscribes to the view that in sheep reduction in growth-rate may be responsible. This reduction

may be due to shortage of feed or to increasing age. Although the underlying reasons for the alteration in coefficient of variability with time remain obscure, it is clear that even under the same conditions of feed, age, and climate it may alter differently in different flocks. Table XVI and Graph No. 4 illustrate the point. The numbers of lambs in each sub-group are rather small, but in this connection the shortage is not perhaps wholly a disadvantage.

TABLE XVI.—STANDARD DEVIATIONS AND COEFFICIENTS OF VARIABILITY OF MEAN WEIGHTS AT DIFFERENT AGES.

Breed.	Age of Ewe and Sex of Lamb.	Standard Deviations.				Coefficients of Variability.			
		Birth.	10 Days.	70 Days.	130 Days.	Birth.	10 Days.	70 Days.	130 Days.
English Leicester ..	Two-tooth—								
	Male ..	0·95	1·97	4·80	5·77	10·33	12·84	10·35	8·3
	Female ..	0·97	2·10	6·43	7·46	10·67	15·00	13·87	11·2
	Four-eight-tooth—								
	Male ..	1·36	2·63	6·90	9·80	13·17	15·16	12·93	12·1
	Female ..	1·04	1·77	6·33	9·22	10·26	10·62	12·54	12·7
	Total ..	1·26	2·54	7·03	10·46	12·85	15·59	14·03	14·2
Southdown	Two-tooth—								
	Male ..	0·89	1·95*	3·85	7·86	8·67	12·79*	7·96	11·6
	Female ..	1·17	2·21	4·92	7·34	15·61	15·40	11·34	11·7
	Four-eight-tooth—								
	Male ..	1·27	2·69	6·84	10·15	14·34	16·08	13·92	14·6
	Female ..	1·02	2·70	4·36	6·60	12·49	16·83	9·41	10·2
	Total ..	1·27	2·69	5·99	9·38	15·49	17·06	12·78	13·8
Romney Crossbred × Purebred Southdown	Four-eight-tooth—								
	Male, "A" ..	1·62	..	4·95	..	14·99	..	9·56	..
	Male, "B" ..	1·62	..	6·05	..	17·35	..	12·36	..
	Female, "A"	1·22	..	4·78	..	11·45	..	9·56	..
	Female, "B"	1·47	..	4·49	..	16·32	..	9·32	..
	Total ..	1·56	..	5·20	..	16·08	..	10·48	..

* = 15 days.

Although the values of the coefficient of variability show the same general sequence for both breeds they are all distinctly different for each sub-group. Sex and age of ewe may have some effect that is at present obscured. Curves plotted from Hammond's data for Suffolk lambs differ distinctly from those for Southdown and English Leicester lambs. It would be idle to suggest various interactions of environment with heredity which might account for the minor variations occurring, but several general features are worth noting:—

(1) The variability usually increases rapidly after birth, but not always. If some of the ewes with heavy lambs—possibly more common among late lambers—milked well and some of the ewes with light lambs milked poorly this result might not be unexpected. Big lambs would then be relatively heavy at 10 days to 15 days, whereas light lambs would be relatively slow growing if their mothers came on milk tardily.

(2) Decreased variability thereafter is in accordance with the theory that variability decreases with growth-rate. The rate of decrease may vary within fairly wide limits.

(3) The observed variability does not always decrease with age. The Southdowns and English Leicesters appear to have responded differently to circumstances between the ages of 70 days and 130 days.

(4) There is no significant difference in values of coefficient of variability for English and Southdown lambs as a whole.

There is clearly a large amount of variation representing the interaction of the individual at different stages of its life with environment which cannot be attributed to any particular cause. To estimate more accurately the effect of any given variable there would have to be an improved knowledge of the causes underlying this residual variation and their interaction with the variable under consideration.

(10) REDUCTION OF VARIANCE.

In estimating the number of animals necessary to show whether a certain treatment or effect has or has not some real influence on the growth or development of a flock, a knowledge of the variation occurring under standard conditions is most useful. For this purpose the standard deviations given in Table XVI give an indication of the values that may be encountered in a flock at different ages and in different localities.

It will be observed that although the standard deviations and coefficients of variability vary from group to group they resemble each other fairly closely. With this information it is possible to calculate approximately how many lambs would be required to show a given difference or, conversely, how great a difference could be shown by the numbers available.

Using the data given previously (Table XVI) the estimates of Table XVII might be expected under some conditions to be fairly accurate.

TABLE XVII.—ESTIMATES OF MEAN WEIGHTS, STANDARD DEVIATIONS, AND COEFFICIENTS OF VARIABILITY FOR RAM LAMBS (SINGLES) AT DIFFERENT AGES, AND ESTIMATED NUMBERS OF LAMBS REQUIRED TO SHOW VARIOUS PERCENTAGE DIFFERENCES.

Estimates for Ram Lambs.	Age.							
	Birth.		10 Days.		70 Days.		130 Days.	
Mean weight	10 lb.		15 lb.		50 lb.		70 lb.	
Standard deviation ..	1·3		2·6		7·0		10·0	
Coefficient of variability	13 per Cent.		17·3 per Cent.		14 per Cent.		14·3 per Cent.	
Percentage Difference from Mean of Ram Lambs.	Difference in lb.	Number required.	Difference in lb.	Number required.	Difference in lb.	Number required.	Difference in lb.	Number required.
2	0·2	338	0·3	600	1·0	392	1·4	408
4	0·4	85	0·6	150	2·0	98	2·4	102
6	0·6	38	0·9	67	3·0	44	4·2	45
8	0·8	21	1·2	38	4·0	25	5·6	26
10	1·0	14	1·5	24	5·0	16	7·0	16
15	1·5	6	2·3	11	7·5	7	10·5	7
20	2·0	3	3·0	6	10·0	4	14·0	4

These numbers are based on a standard error of the difference, which is just half the difference given.

Supposing that a difference of 6 per cent. in weight of ram and ewe lambs were expected the table shows that thirty-eight lambs of each sex would probably give statistically significant results. On the other hand, if only about twenty of each sex were available, differences of less than 8 per cent. would probably not be satisfactorily established. This example also makes clear a particular use of the coefficient of variability. As it rises in value (as at tailing) the number of animals necessary increases rather rapidly. Its reduction is therefore desirable.

There are so many respects, however, in which lambs within a flock receiving one treatment may differ that the use of groups differing in one respect only is prohibited by their almost inevitably small size. It has been shown by various authors that sex, number of offspring, age of ewe, weight of ewe, time of birth, and various other factors affect the growth of lambs. Some of these have been examined under Canterbury conditions and found to have appreciable effects. The comparison of groups differing in any of these respects must yield misleading results, and frequently obscure real differences which exist, unless their effects are measured and allowed for.

It has been shown above that a large proportion of the total variation which occurs has to be included in the general term of "error variance." The greater the amount of variation which is unaccounted for the greater the size of the flocks necessary in experimental work. Doubtless much variability is genetic in origin. Chapman and Lush(8) found that differences between twins accounted for 44–48 per cent. of the total variation shown by all twin lambs, so that the use of genetically similar sheep would be a considerable advantage if it were possible to get them.

Whilst it seems fairly certain that the technique of weighing, feeding, &c., is responsible for some variation, which is therefore reducible by better methods (Dunlop(7)), the allowance for known variables should be made by methods available now. The reduction in total variance brought about by eliminating two important causes of variation has, in this study of growth-rates in lambs, sometimes reached almost 30 per cent.

ACKNOWLEDGMENTS.

The authors are indebted to Professor R. E. Alexander, Director of Canterbury Agricultural College, for permission to carry out this work, and to Mr. A. Leslie, of the Veterinary Department, for much data and helpful criticism. The records of crossbred sheep have been supplied by Mr. Leslie and were collected with the aid of grants from the Meat Producers Board, Agricultural and Pastoral associations, and other farmers' organizations.

The authors are also indebted to Mr. D. J. Sidey for records of birth-weights of Romney Cross × Southdown lambs in 1932 and 1933.

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THE MILK CONSUMPTION AND GROWTH OF SUCKLING PIGS

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THE lightest pigs at, or before, weaning are by no means always the 'poorest doers' in later life. This fact has been indirectly indicated by many who have worked with the correlations between weights at various ages, and the principle receives practical recognition in the grouping of growing pigs according to size rather than age.

The explanation generally accepted is that there are differences between the quantities of milk produced by sows and between the amounts of milk obtained by individual pigs of a litter. Concerning the differences between sows there can be little doubt [1, 2], but for the differences between the quantities of milk obtained by the pigs of a litter the evidence is mainly indirect. During the progress of research work with a Large White herd in Edinburgh, an effort is being made to isolate genetic differences in the growth-rate of pigs from conception to weaning, and for this purpose it has seemed desirable to obtain some direct evidence on the quantities of milk obtained by suckling pigs. In this way it was hoped to determine whether variations in growth-rate could be completely explained by varying levels in food-supply. In contrast to previous investigations of the milk-production of sows, the work here described involved the weighing of individual pigs before and after suckling instead of litter-weighings. For the immediate purposes of the main investigation it is felt that this particular series of observations has been continued long enough, for although some of the outstanding questions have not yet received an answer, progress must be made in other directions before this can be pursued further.

I. THE METHOD

The method adopted was to remove the pigs from the sow 1½–2 hours before the first weighing and thereafter return them to her for suckling only at 2-hour intervals. The greatest difficulty was found to be the tendency of the pigs to urinate after they had suckled, or even to stop suckling to do so, but this was overcome by turning them out of their bedding and making them stand for some minutes in the dunged area of the pen before weighing. Those which had not urinated could be detected by their almost unchanged weight, and were watched. The error arising from this source is considered negligible. The amount of weight lost by urination varied with the size of the pig from about 10–30 gm. Defaecation caused a very slight loss, usually less than 5 gm. After standing the pigs were weighed to the nearest gram. The technique for obtaining the best weight appears to be to use a direct-reading balance (not a spring one), damp the movement down somewhat, and be prepared to read off the weight quickly. The pigs were then

delivered together to the sow. Suckling took place promptly and the p were removed as soon as their behaviour showed that the udder empty. During suckling, the position of each pig on the udder was no at intervals by means of a system of easily recognized black dots pain on the pigs. The pigs were then weighed again as quickly as possib

TABLE 1. *Samples of Results obtained by Weighing before and after Suckling (from periods of continuous observation)*

Difference in grams before and after suckling

Pig No.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
Litter 1 .	2	37	−10	34	29	28	23	9	19	..	32	34
	−1	39	26	49	35	38	−4	23	29	27	36	32
	10	40	21	23	38	38	15	41	29	28	31	45
	7	40	25	46	30	38	31	32	27	−2	29	40
	15	31	1	20	34	−10	..	32	−9	−11	−1	35
	34	187	73	172	166	142	69	137	104	55	128	186
Litter 2 .	47	30	7	20	29	25	5	4	35	5	21	49
	57	36	64	20	36	32	..	7	2	55	..	..
	22	19	65	29	8	31	..	45	80	10	23	..
	4	39	30	31	25	15	38	50	..	18	15	36
	55	13	55	1	9	73	3	22	67	40	55	23
	60	36	14	24	35	40	..	27	35	2	16	17
	245	173	235	125	142	216	46	155	219	130	130	125
Litter 3 .	60	55	100	49	35	73	54	67	52	36		
	83	56	85	58	30	66	71	83	35	36		
	73	43	70	54	27	67	74	72	37	34		
	84	58	90	69	24	66	81	88	47	42		
	67	43	82	61	24	83	77	82	42	41		
	85	61	89	67	35	82	78	78	49	32		
	452	316	516	358	195	437	435	470	262	221		

Litters 1 and 2 were in the first group of experiments, Litter 3 in the second.

The first suckling was often unsatisfactory because both sow and lit were disturbed by the unusual treatment. The rate of adjustment both sides, however, was remarkably rapid, and whenever continuo observations could be taken the results were surprisingly good provid there was no disturbing feature, such as ailing pigs. The small p showed marked differences in their reaction to the necessary handli The records in Table 1 show that Nos. 1 and 13 in the first lot, and 7 a 8 in the second lot did not obtain their share of milk during the first f sucklings, but whereas the reason was probably severe competition w the first two, which were the lightest in the litter, this would not ap to the second two, which were the second and third heaviest. Large p were often found to take no interest in the proceedings until time brou on a sufficient hunger to overcome whatever disinclination to suc existed. 'No change' in weight was often recorded. An increase or crease of one or two grams was accounted for by the error in weighi and is considered as evidence that no milk was obtained. Occasionally, course, the amount of milk obtained would be offset more or less by t weight loss by urination. The usual causes of no change are, howe

failure by the pigs to suckle promptly and vigorously, and fighting over the possession of a teat. Owing to the very short time during which the milk is liberated by the sow, a pig has to be ready and willing, otherwise the opportunity will be missed.

II. RESULTS

The experiments may be divided into two groups. The first involved observations made only during the day, the pigs being returned to the sow during the night; the second consisted of continuous observations on two sows for a week. The former will be dealt with briefly, as the results obtained were essentially the same as those from the second group, which was the more satisfactory as it gave a complete record.

The type of results found when only daytime records were made is exemplified in Table 2. It will be observed that in spite of the incompleteness of the records, there is a considerable degree of similarity between the amount of milk obtained and the weight and gains of the pigs. All deductions from this table are subject to the proviso that the amounts of milk obtained during the periods of non-observation were of the same proportions as those obtained under observation. The table, with this proviso, does suggest that the large pigs get more milk than the small, that the rate of gain is closely associated with the amount of milk obtained, and that there may be differences in the efficiency $\left(\frac{\text{Increase in wt.}}{\text{Amount of milk}}\right)$ with which the pigs deal with their food-supply.

TABLE 2. *Comparison of Weight of Milk, Weight of Pigs, and Increase in Weight during Period of 29 Sets of Weighings*

(The columns headed 'order' classify the data in the preceding columns in order of magnitude)

Amount of milk gm.	*Order*	*Wt. at start of weighing kg.*	*Order*	*Wt. at end of weighing kg.*	*Order*	*Increase in wt. kg.*	*Order*	*Ratio: inc. in wt. to amt. of milk*
1,143	1	1·737	6 =	2·844	4	1·107	4	0·97
1,080	2	1·747	4	3·114	2 =	1·367	2	1·27
1,027	3	1·822	2	3·260	1	1·438	1	1·40
1,002	4	1·776	3	3·114	2 =	1·338	3	1·34
913	5	1·586	8	2·539	6	0·953	5	1·04
885	6	1·868	1	2·692	5	0·824	6	0·93
825	7	1·737	6 =	2·493	7	0·756	8	0·92
793	8	1·325	10	2·095	9	0·770	7	0·97
747	9	1·740	5	2·401	8	0·661	9	0·88
697	10	1·296	11	1·950	10	0·654	10	0·94
439	11	1·442	9	1·928	11	0·486	11	1·11

In order to determine these points with more certainty, it was decided to carry out complete observations over a period. Two sows with 3-week-old litters were chosen. The sows were even-tempered and soon became used to the treatment. One was raising her third litter and the other was a gilt which had already been observed intermittently. Suckling took place at intervals of approximately two hours during the day, and 3 hours during the night. A sample of the results is given in Table 1 (litter 3) which shows clearly that there is much similarity in

the consecutive amounts of milk obtained, some pigs receiving alw a large amount and others a small amount. Two small pigs in the g litter were in the process of losing the struggle for existence, fallin weight owing to repeated failure to secure a teat, and becoming less less able to assert themselves. One pig of the other litter, No. 4, had injured front hoof and was handicapped to some extent by that, altho it succeeded in retaining its own teat throughout.

The relation between the weight of the pigs, the increase in wei and the amount of milk obtained (together with two estimates of ciency) are given in Table 3.

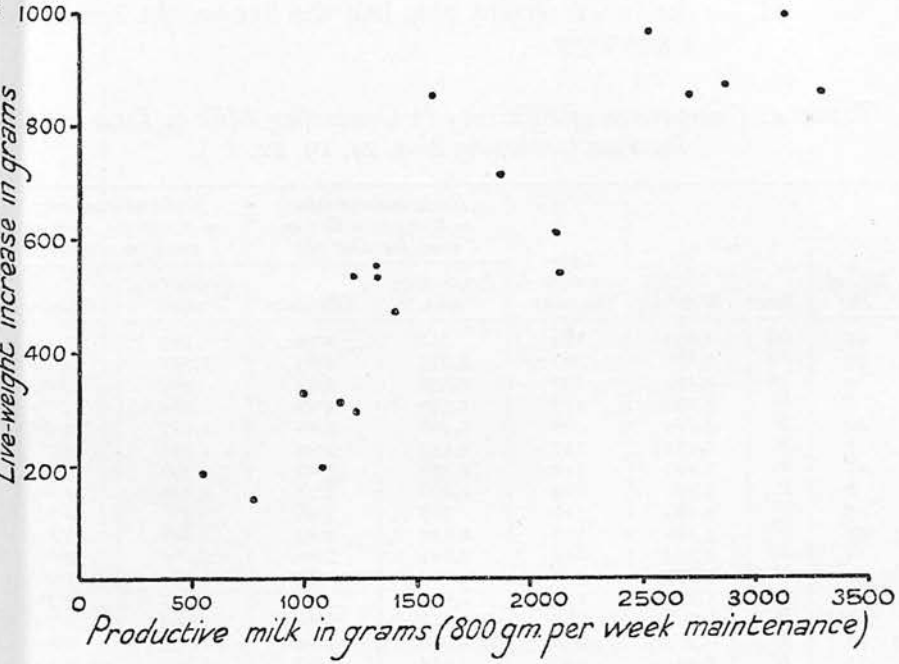
TABLE 3. *Relation between Weight of Pig at Start of Experiment, Increase in Weight, and the Amount of Milk obtained (based on 74 observations during 7 days)*

No.	*Sex*	*Weight at start gm.*	*Order*	*Increase in weight gm.*	*Order*	*Amount of milk gm.*	*Order*	*Efficiency Quotient, E.Q.**	*Ratio: in wt. Amt. of*
1	F	6,371	1	852	4	5,251	1	11·01	0·16
2	M	6,358	2	960	2	4,480	4	14·63	0·21
3	M	5,988	3	985	1	5,012	2	12·77	0·19
4	F	5,310	4	845	5	4,421	5	10·95	0·19
5	F	5,123	5	140	10	2,373	10	3·06	0·05
6	F	4,996	6	862	3	4,524	3	10·37	0·19
7	F	4,776	7	537	8	3,717	6	7·31	0·14
8	M	3,956	8	550	7	2,712	8	8·59	0·20
9	M	3,938	9	530	9	2,707	9	8·24	0·19
10	M	3,513	10	707	6	3,169	7	8·62	0·22
11	M	6,423	1	534	3	3,160	3	11·30	0·16
12	F	5,882	2	850	1	3,412	2	15·70	0·24
13	F	5,795	3	605	2	3,917	1	9·39	0·15
14	F	5,785	4	43	10	2,666	9	0·92	0·01
15	M	5,611	5	198	8	2,808	6	4·05	0·07
16	F	5,407	6	531	4	2,704	8	11·12	0·19
17	F	5,136	7	292	7	2,860	5	5·39	0·10
18	F	4,935	8	510	5	2,761	7	9·60	0·18
19	F	4,873	9	..	..	..	..	..	..
20	F	4,641	10	466	6	2,933	4	7·75	0·15
21	F	2,955	11	−126	..	883	11	..	..
22	M	2,566	12	186	9	1,496	10	3·30	0·12
23	F	2,025	13	..	..	..	..	..	..

* E.Q. $= \frac{\text{Increase}}{\text{Amount of milk}} \times \frac{\text{Weight}}{100}$; Weight = (initial weight + ½ live-weight increase d the experiment).

In this table the pigs are arranged in order by weight within litt numbers 1–10 belonging to the older sow's litter and numbers 11 to that of the gilt. No. 5, which was lame, suffers as a result in comp son with the others. When the experiment began Nos. 19, 21, and were falling behind their litter-mates in size and getting progressiv less milk, so that they shortly became so weak that they stood no cha at all. At the end of the week they were still alive and responded rap to a little preferential treatment. In the sow's litter, the relation betw size of pig, increase in weight, and amount of milk is quite close. In gilt's litter it is also reasonably close, considering the defections and failure of No. 14 to make much headway. On the whole, the conclusi of Carlisle [3], Bonsma and Oosthuizen [2], Thompson [4], and oth that the largest pigs in a litter obtain the most milk are borne out. Th

ppears to be an even closer proportionality between the increase in live eight and the amount of milk obtained, and the question arises whether he larger pigs with their greater rations are more or less economical han the smaller pigs. Bonsma and Oosthuizen were led by their data o ask the same question. As a first step towards the answer the last two olumns were calculated, the Efficiency Quotient (E.Q.) after the nanner of Palmer and Kennedy modified by Winters and McMahon



GRAPH 1. Relation between Live-weight Increase and Amount of Productive Milk consumed (maintenance of 2kg. pig for a week assumed to be 800 gm. of milk)

[5]. Now although according to E.Q. the largest animals were the most efficient, the same clear superiority was not shown when body-weights were left out of account, as in the last column. In order to reconcile these figures the question was approached from another angle, viz. by estimating the maintenance-requirement in terms of milk for each pig and using the quantity obtained in excess of this (called productive milk) for the efficiency calculation, efficiency being defined as the ratio of productive milk to live-weight increase, or the number of grams of productive milk required for 1 gm. live-weight increase. The smaller the number, the more efficient the pig. Unfortunately, determinations of the maintenance-requirements of such small pigs could not be found, and had to be deduced indirectly. As a first approximation it was assumed, after Schneider [6], that roughly 2 gm. of milk would be needed to give 1 gm. live-weight increase, and working backwards we obtain 1,000 gm. of milk as the approximate maintenance-requirement of a 2 kg. pig for a

week. Five values between 800 and 1,200 gm. were then tried to see which produced the most reasonable range of efficiencies. This was done by calculating the maintenance for each pig from each of the five basic maintenance-requirements from the formula:

$$\text{Maintenance-requirement} = M_b\left(\frac{W}{2{,}000}\right)^{0.73},$$

where M_b = 800, 900, 1,000, &c.,
W = the initial weight plus half the live-weight increase of a given pig.

TABLE 4. *Comparison of Efficiency in Converting Milk to Live-weight Increase (excluding Nos. 14, 19, 21, 23)*

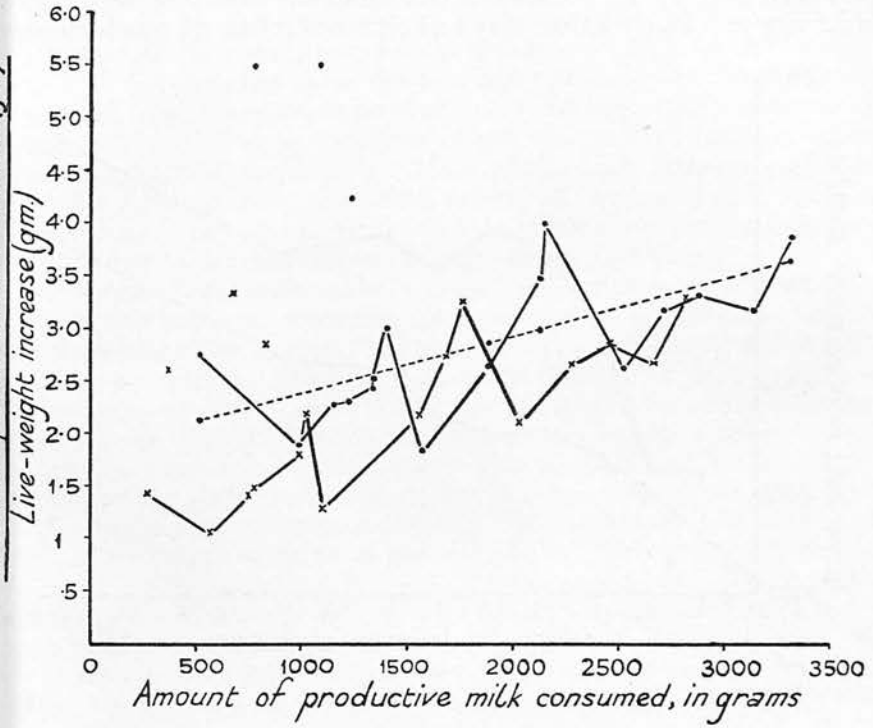
No. of Pig	Sex	Weight	Live-weight increase	Basic maintenance = 800 gm. milk per week for 2 kg. pig		Basic maintenance = 1,000 gm. milk per week for 2 kg. pig	
				Productive milk	Efficiency	Productive milk	Efficiency
22	M	2,659	186	511	2·75	265	1·43
10	M	3,867	707	1,875	2·65	1,551	2·19
9	M	4,203	530	1,331	2·51	987	1·86
8	M	4,231	550	1,330	2·42	984	1·79
20	F	4,874	466	1,400	3·00	1,017	2·18
7	F	5,045	537	2,145	3·99	1,752	3·26
18	F	5,190	510	1,157	2·27	756	1·48
6	F	5,427	862	2,866	3·32	2,452	2·84
5	F	5,193	140	767	5·48	366	2·61
17	F	5,282	292	1,234	4·23	828	2·84
4	F	5,733	845	2,695	3·19	2,264	2·68
16	F	5,672	531	992	1·87	564	1·06
15	M	5,710	198	1,087	5·49	657	3·32
13	F	6,098	605	2,111	3·49	1,660	2·74
12	F	6,307	850	1,562	1·84	1,099	1·29
3	M	6,481	985	3,125	3·17	2,653	2·69
2	M	6,838	960	2,518	2·62	2,027	2·11
1	F	6,797	852	3,297	3·87	2,808	3·30
11	M	6,690	534	1,229	2·30	746	1·40

All weights in grams.

In accordance with the results of Brody, Procter, and Ashworth [7] maintenance is presumed to be proportional to the 0·73 power of the weights. The most reasonable results were given when 800 gm. was taken as the basis, the others resulting in efficiencies which appear too high. As a check on these figures, the basal metabolism for a 2- animal given by Brody, Procter, and Ashworth, viz. 117 Calories day, was converted into grammes of milk per week. If 1 gm. of digestible milk nutrients is equivalent to 4 Calories, and if in sows' milk there are 25·5 per cent. total digestible nutrients, 803 gm. of milk per week would be required. This is sufficiently close agreement. The purpose being to expose differences in efficiency rather than the actual value, does not greatly matter whether this is an accurate estimate or not provided there is a basis for comparison. Table 4 and Graph 2 show that

even if 1,000 grams is used as the basic figure, there is little change in the relative performances of the pigs.

Table 4 provides a comparison of efficiencies estimated in this way. The relation between the amount of milk available for growth and the actual increase in weight is brought out more clearly in Graph 1, which shows a strong correlation between the two. It also conveys the

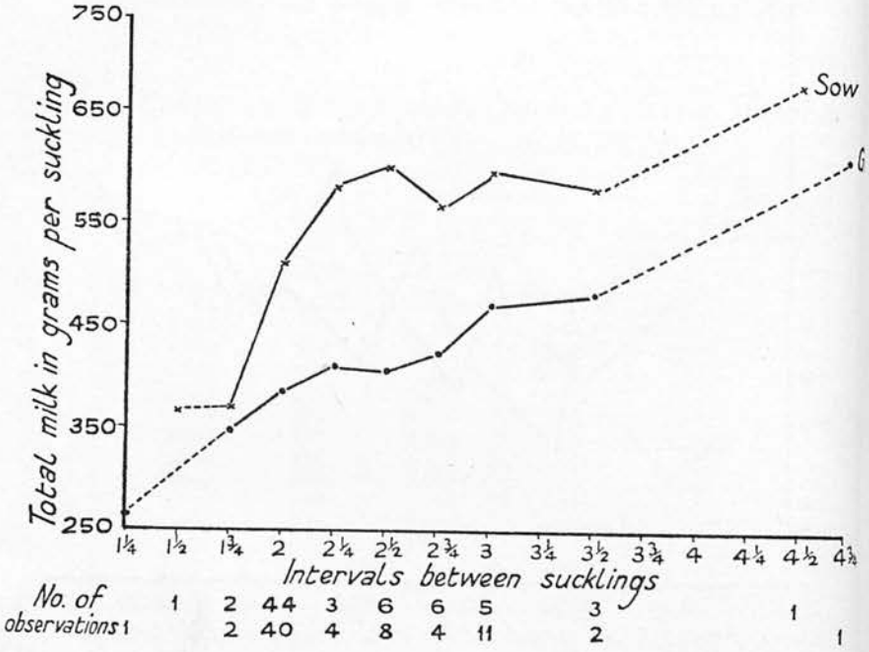


GRAPH 2. Relation between Total Amount of Productive Milk Consumed in Seven Days and the Amount of it Required per Unit Live-weight Increase.

——×—— maintenance-requirement 1,000 gm. milk per week for 2 kg. pig
——·—— " " 800 gm. " " " "
- - - - - - - regression of $\frac{\text{productive milk consumed}}{\text{live-weight increase}}$ on amount of productive milk when maintenance-requirement is 800 gm. milk per week. The value of the regression coefficient is 0·52 for a change of 1,000 gm. in the amount of productive milk consumed, and its significance is beyond the 1 per cent. point. The calculation has not included the three aberrant results.

suggestion that the animals receiving the most milk in excess of their maintenance-requirements, were converting it less efficiently than those receiving less. By plotting productive milk against efficiency this can be detected more easily (Graph 2). If efficiency were the same for all levels of feeding, the curve should remain approximately horizontal. Since the curve drawn from the observations (but excluding three of them) shows a definite upward slope, it would appear to indicate that the pigs which

had the largest amounts of productive milk, were making less economi use of it than the pigs which had less. This conclusion is vitiated c siderably by two of the three observations which were not introdu into the curve and have been shown separately. The third one was fr the lame pig and could be justifiably omitted, but for the other two suitable explanation is forthcoming. The pigs involved were Nos (the lame pig), 15, 17. The other two could not have possessed such l efficiency previously unless they had obtained relatively much more m



GRAPH 3. Relation between Length of Interval between Sucklings and Amoun Milk obtained by the Litter.

than their litter-mates, or they would not have had so large an ini weight. Even if they were included in the curve of Graph 2, howe the rise would still be apparent although not as steep as shown.

Effect of time between sucklings on the amount of milk obtained.—I though the aim was to space sucklings at 2-hour intervals during the d and at 3-hour intervals during the night, these could not always exactly observed, so that there is a range of intervals of varying len for comparison of the total amounts of milk obtained by the litter. T results are shown in Graph 3. In addition to the obvious difference the yield of milk from the sow and the gilt (from Table 3; total mi sow 38·4 kg.; gilt 29·6 kg.), there is a clear indication of an increase in t amount of milk with longer intervals between sucklings: all the te showed increased amounts. This is to some extent in accord with t results obtained with cows. At the end of the experiment the s was giving rather more milk than at the beginning, and the gilt rat

less. This is entirely to be expected from normal changes during the progress of lactation, and there is no evidence that the unusual treatment 'put the sows off their milk'.

The figures available are scarcely adequate to show where lies the upper limit to the amount of milk which the udder can hold. Were it not for the two exceptionally long intervals the conclusion might have been drawn that these limits were probably in the neighbourhood of 600 gm. for the sow and 500 gm. for the gilt. That they can hold more than this is clear enough. The maximum for the sow at any weighing was 691 gm. and the gilt 635 gm., but these values might not represent the maximum determined from numerous observations. The explanation is favoured that the interval between sucklings affects the yield of milk, although another explanation is possible. Most of the long intervals occurred during the night, and the short ones during the day, so that if darkness were associated with higher yield, such an effect could not be separated from that due to the differences in length of the intervals.

Distribution of milk in the udder.—It has been pointed out on numerous occasions that the 'best' teats are the forward ones. That mere inspection shows this to be subject to exceptions does not detract much from its value as a generalization. Quite large differences in the yield of different sections of the udder which are not apparent to the eye would appear to exist. Not only in the two sows under discussion but in various others it has been noted that although it is possible to tell a manifestly good mammary gland from a poor one, it is not easy to place them all in their correct order according to yield. As an example the distribution of milk in the udder of the older sow is given in Table 5: similar data for the gilt are not presented as her pigs did not suck as consistently at the same teat. The last two pigs suckled a pair of teats each. Although the largest yield was obtained at the anterior end, there was in this case no clear gradation from one end to the other, nor was there close agreement between the yields from members of each pair of teats.

TABLE 5. *Distribution of Milk in the Udder of the Sow. Total Milk (in gm.) from each Teat for the Week of Observation*

Teat No.	*1 anterior*	*2*	*3*	*4*	*5*	*6 posterior*
Right side	4,381	4,480	2,373	4,334	3,717	2,707
Left side	5,201	3,169	4,862	2,572		

Discussion

The effect of an investigation such as this is to invite reconsideration of the importance of variability in weaning or 3-week weights. Differences in size among young pigs are probably useless for comparing their genetic qualities. Such differences as have been found, and even some deaths, can be satisfactorily explained by variation in the level of nutrition. These differences are disadvantageous not only from the point of view of husbandry, and economy, but they must remove the possibility

of making any early judgement concerning type, owing to the differ relative growth-rates of the parts of the body at different ages [8].

The positive correlations between weights at various ages [9], wh might be attributed to qualitative differences in the pigs, may me measure the advantage at any age of superior weight. On the ot hand the decrease in size of the correlation coefficients as the pe between the weighings increases, must mean that advantage in we is often lost. This may be accounted for partly by accidents, and pa by efficiency changes induced by variations in the quantity or quali the food. The negative correlation between average daily gain f birth to weaning and weaning to slaughter found in calves by Black Knapp [10] is probably evidence of the latter. It would be surpri indeed if the animals which were best fitted, in the genetical sense, intra-uterine life, were also the best fitted for growth on a grain after so short a period of adaptation as has elapsed since modern feedi methods were available.

That selection of animals in order to increase the average performa over the whole lifetime must be an exceedingly difficult and slow proc can be appreciated by considering for a moment selection for performa during a restricted period of life, such as the first three weeks after bi As was shown in Table 4, there are considerable differences in the econo with which pigs convert their food into live-weight gain. Such diff ences, if genetic, might be due to relatively high or low maintenan requirements, early or late onset of diminishing response to increme in the amount of food, and so on. Each of these possible causes co be further subdivided into numerous parts, such as variations in dispo tion to exercise, in chemical composition, and temperature-regulati Ultimately large numbers of genes must be involved, and large numb of different genotypes must have indistinguishable phenotypes. Eve the really superior animals could be detected, selective breeding co accomplish improvements only very slowly [11], unless some few ge with major effects prove to be involved. In that event, the prosp of accumulating them is much brighter, and the search for means identifying them justified. Grounds for believing that this may be is provided by the experience of Morris, Palmer, and Kennedy [1 who were able to establish lines of rats significantly differing in rate growth.

The foregoing results also suggest some comments on the use litter-weights as measures of the milking-capacity of the sow. If t subjects of the present experiments exhibit the working of a gene law of diminishing response to increments of food, the fact would h to be recognized in evaluating the performance of sows and litt Although the relative decrease in maintenance-requirement with incre ing weight offset to some extent the loss of efficiency in the pigs wh received the most productive milk, the effect was not considerable wh the rate of growth was reasonably rapid. A difference of 1 kg. in weig between two light pigs in a litter would therefore represent much l milk than the same difference between two heavy pigs. This co account for the comparatively small reduction in the average weight

three weeks with increasing litter-size shown by Johansson's data [13]. It seems probable that the average amount of milk per pig would show a much greater reduction with increasing litter-size.

If experience with milking cows counts for anything in breeding for milk-production in pigs, it is most desirable to obtain outstanding per- formers for grading up a herd. It may be unfortunate that these should have to be detected by means of the weights of their litters, for unless the herd performance is rather low, the differences in milk-yield between good and outstanding sows may not be associated with corresponding differences in litter-weights. Considering possible variations in litter-size and number, seasonal fluctuations, and accidents, they may well be undetectable. Another consequence of these results would be that litter- weights must mask to some extent (obviously not completely) the actual range of variation occurring in milk-production. Still more justification would then be forthcoming for drawing an analogy between present herds of breeding sows and the herds of milking cows of pre-testing days.

Since small pigs are more economical converters of solid food than their mothers, there would be no point in striving after phenomenally produc- tive sows except for breeding purposes. All that is required is that a sow shall have milk enough to carry her pigs through the stage of transi- tion to solid food without check. This means that not only the peak production as measured by three-week weights, but also persistency as measured by later weights, should be considered. It may well be that in the future the suggestion of Asdell [14] that the inheritance of the components of milk-yield rather than total yield should be studied, will have to be heeded.

Summary

1. An experiment is described in which two litters of Large White pigs were weighed individually before and after each suckling for a week. A close association was found between the live-weight increase and the amount of milk consumed.

2. One sow which was nursing 10 pigs in her third litter gave over 30 per cent more milk than the other sow which had 12 pigs in her first litter.

3. In general the largest pigs in a litter obtained the most milk. If certain assumptions are made concerning the amount of milk required for maintenance, the pigs which received the most milk in excess of their maintenance-requirements appear to have converted it to live-weight increase less economically than their litter mates.

4. As the interval between sucklings lengthened, the amount of milk obtained by each pig increased. For one of the sows the actual production for each nipple could be ascertained and showed great irregularity. The anterior nipples tended to be more productive than the posterior.

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SUCKLING AND SUCKLING PREFERENCE IN PIGS

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[T is often asserted that during the suckling period each member of a itter 'has its own teat', i.e. suckles regularly at a particular nipple. This suckling preference' is not without practical interest, for it would mean hat some pigs in a litter would obtain very much less milk than others ince different gland sections of the udder may secrete very different uantities [1]. There is, however, little or no information concerning he extent of this preference. As it has an obvious bearing on the ariability of litter-mates, a problem which is receiving attention in the arge White herd of the University of Edinburgh, a series of observaions has been carried out to provide an estimate of its significance. ome preliminary experiments have also been made to determine what actors influence the choice of nipple; the results, although not particuarly important in themselves, suggest that the sow and litter provide most interesting and instructive material in the study of animal ehaviour. In addition to an account of these observations and experients, the present paper includes some comments on the process of uckling, which has been frequently and closely watched.

The term 'suckling preference' disguises the fact that there are at east two kinds of preference, which may or may not be antagonistic. he first is shown by all pigs from the moment of birth in their attempts o attach themselves to the anterior rather than the posterior nipples. he reason for this will be discussed later. Tsai [2] found that young ats suckled most frequently at the fourth pair of nipples. He suggested hat, having regard to the suckling attitude of the female rat, this pair as the most accessible. This type of preference is distinguishable from he second type, which markedly affects the distribution of pigs along he udder of a sow, and arises from a desire among pigs to suckle each at particular nipple, a desire which apparently does not exist in litters of ats. Suckling preference in this sense has been referred to by many uthors including Carlisle [3], Hempel [4], Bonsma and Oosthuizen [5], ugenroth [6], Fishwick [7].

Material and Method

The sows and litters upon which the following observations were ade included some which were utilized also for obtaining estimates of ilk-production and were therefore of a quiet disposition, but otherwise here is no reason to suppose that the results may not be typical. The gs were recognized with the aid of spots painted on them. It was not ways possible to make observations of undoubted accuracy; sometes the sow would be fidgety; sometimes a pig would try several teats; nd sometimes it would be obscured by a litter-mate. Errors of observaon arising in this way are not considered sufficient to make any real

difference to the results, nor are errors due to the impossibility of be sure that pigs in the lower row were actually suckling a nipple wi observed.

Results

Altogether 97 sets of observations have been made on 5 sows v litters. As almost any one litter would serve to illustrate the main c clusions of this study, it is not proposed to present the whole of the nor any of the more fragmentary observations which support the re obtained. The data contained in the following tables do not there represent the complete material on which the conclusions are base

Table 1 clearly shows that there is a firm foundation for the belief each pig in a litter 'has its own teat'. To simplify matters, only t observations were included during which the sow was lying on her r side. The 'correct' positions of the pigs have been assumed to be t most commonly occupied, and have been distinguished as R1, R2, ... on the right side, and L1, L2, . . . L6, on the left side. Pigs wi positions were therefore suckling the nipples next to the ground.

TABLE 1. *Positions occupied by the 10 Pigs (aged 3–4 weeks) in the L of Sow* A *during 21 Sets of Observations (Sow lying on her Right Sid*

Pig No.	*Weight*	*Correct position*	*No. of times*		*Incorrect Positions*
			Correct	*Incorrect*	
	kg.				
1	6·7	L1	21	0	
2	5·6	R1	20	1	R2
3	3·8	L2	20	1	L3
4	6·6	R2	17	4	L2, R3, R5, R1
5	6·3	L3	19	2	L2, R2
6	5·2	R3	16	5	R2, R4 (2), L4,
7	4·2	L4	21	0	
8	5·3	R4	19	2	R3, R5
9	4·9	L5, R5	21	0	Yielded R5 on sions to Nos.
10	4·1	R6, L6	21	0	
		Total	195	15	

Nos. 9 and 10 each suckled a pair of nipples.

When a wrong position was taken up by one pig, another pig was us but not always, also out of position. In some instances, two pigs w endeavour to obtain the same nipple, and only one mistake was de to have been made if one of the pigs was the rightful owner. Dis ment of this kind occurred usually when one pig could not find its or a vacant position and attempted to take another by force. tenacity with which the original occupier would resist such in and refuse to be satisfied with any other position is to be contrasted a much greater readiness to suckle the 'wrong' teat when unable t its own.

The general conclusion that the pigs at either end of the udd rarely found out of position is well illustrated by this litter. Most

errors have been committed by Nos. 4 and 6, the other pigs being forced into secondary errors. In all litters the pigs centrally placed were most often at fault, suggesting that it is more difficult to find a correct position in the middle than at the ends of the udder. In this particular litter, it is not without significance that Nos. 4 and 6 belonged to the lower row of teats, for their difficulties were thus increased.

It will be observed that most of the errors were horizontal ones, i.e. when a pig did take a wrong nipple, it chose one in the row in which it customarily suckled. From this it may be supposed that a habit of suckling either standing or crouching may be formed by some pigs. This conclusion would not have been so clear if this particular sow had not been in the habit of lying on her right side. It is to this habit that the comparatively low percentage of errors found in this litter can be attributed. What was involved seemed less to be 'right-sidedness' than good mothering, for the sow frequently lay down on her left side, but only once in 24 recorded sucklings actually suckled her pigs that way. Whenever she lay on her left side there was much confusion amongst the pigs, and she regularly got up and lay down on her right side to cure it. Although the figures are not extensive enough to prove it, there is a strong suspicion that some of the other sows were also more inclined to lie more often on one side than the other. One sow (B), for instance, was observed seven times on her left and twice on her right; her eleven pigs made no errors at all while she was on her left, but re-arranged themselves to some extent when she lay on her right.

An interesting point is raised by the nature of the re-arrangement occurring when a sow which lies usually on one side, tries the other. It might be expected then that a pig which had become accustomed to standing in the upper row of nipples or to lying in the lower row, would have to choose between retaining its accustomed nipple or its accustomed position. On the five occasions on which the pigs in the litters of Sows A and B were observed making this choice, about half the pairs elected to change sides and retain their own nipples, and about half took up their usual positions and accepted the strange nipples. Since they were not consistent in their choices, it would appear that both position of body and recognition of nipple as well as the appreciation of horizontal distances play a part in determining the disposition of pigs at suckling.

The behaviour of a litter under rather more complicated circumstances is recorded in Table 2. In this case the sow (C) was raising her first litter of nine pigs together with four others which had been transferred to her for another purpose. She differed from Sow A in several respects. She lay readily on either side, she turned a deaf ear to fighting amongst her pigs, and she presented a smaller udder to thirteen pigs as compared with the ten of Sow A, on a large udder. Three sets of observations were made at intervals of about a fortnight, the first being made on the fourth and fifth days after farrowing.

There can be little doubt that as early as the fourth day after farrowing, the litter had distributed itself into positions that were retained for the most part until at least one month later. The extent to which this litter

gradually became more accurate in discovering the appropriate positions may be roughly measured by the percentage of the observations at each age which agreed with the 'correct', i.e. the most common, position at one month old. At 4–5 days old 40–50 per cent. of the observed positions were the same as the 'correct' positions at 1 month old; the corresponding value at 2 weeks old was slightly more than 50 per cent., and

TABLE 2. *Positions occupied by the Pigs in the Litter of Sow* C *as observed at Three Different Periods of Suckling Separated by Intervals of about a Fortnight*

(Column 2 shows on which side sow was lying)

No. of pig	*	*20/4–21/4*		*2/5*		*16/5–20/5*
1	R	R1 (4) L1 (2)	6	R1 (6)	6	R1 (9)
	L	R1 (2) L1 (1)	3	R1 (1)	1	R1 (10)
2	R	L1 (4) R1 (2)	6	L1 (6)	6	L1 (10)
	L	L1 (2) R1 (1)	3	L1 (1)	1	L1 (9)
3	R	L2 (5) L3 (1)	6	L2 (6)	6	L2 (7) L3 (1)
	L	R3 (3)	3	R2 (1)	1	R2 (7) R3 (2)
4	R	R2 (4) R4 (1) L2 (1)	6	R2 (3) R3 (2) R7 (1)	6	R2 (6) R3 (4)
	L	L2 (2) R2 (1)	3	L2 (1)	1	L2 (8) L3 (1)
5	R	R3 (4) R4 (2)	6	R3 (2) R4 (2) R2 (1) R5 (1)	6	R3 (4) R4 (2) R2 (3)
	L	L3 (1)	1	R3 (1)	1	R3 (6) R2 (1) L2 (1) L3 (1) L4 (1)
6	R	R2 (2) R5 (1) R4 (1)	4	R6 (3) R5 (2) L3 (1)	6	L3 (8) R1 (1) L2 (1)
	L	L3 (2) L2 (1)	3	R7 (1)	1	L3 (6) L2 (1) R4 (1) R5 (1)
7	R	L3 (4) R4 (1) L6 (1)	6	L3 (3) L4 (2) R4 (1)	6	R4 (4) R3 (2) L2 (2) R2 (1)
	L	R4 (2) L4 (1)	3	R4 (1)	1	R4 (7) R2 (1)
8	R	R3 (2) L3 (1) R5 (1) L5 (1)	5	R3 (2) R4 (2) L3 (1) R5 (1)	6	L4 (8) R4 (1)
	L	L4 (1) R2 (1) L6 (1)	3	R5 (1)	1	L4 (3) R4 (1) R5 (1) R6 (1)
9	R	R6 (2) L4 (2) R4 (1) R5 (1)	6	R5 (2) R6 (2) L5 (1) R7 (1)	6	R5 (8) R4 (1) R6 (1)
	L	R5 (2) R6 (1)	3	L3 (1)	1	R5 (6) R4 (1) R6 (1) L4 (1)
10	R	L4 (3) L5 (2) R6 (1)	6	L5 (6)	6	L5 (8) R4 (1)
	L	L5 (2) R6 (1)	3	L5 (1)	1	L5 (6)
11	R	R7 (4) R5 (1) L5 (1)	6	R7 (4) R6 (1)	5	R6 (1) R5 (2)
	L	R6 (1) R7 (1) L5 (1)	3	R6 (1)	1	R6 (6)
12	R	L6 (4) R6 (1) R7 (1)	6	L6 (6)	6	L6 (9) R7 (1)
	L	L6 (2) R7 (1)	3	L6 (1)	1	L6 (8) R7 (2)
13	R	R6 (1) R7 (1) L5 (1) L6 (1)	4	L4 (3) R2 (1) R4 (1) R7 (1)	6	R7 (4) L3 (1)
	L	R7 (1) R4 (1) L4 (1)	3	L4 (1)	1	R7 (4) L6 (1) R2 (1)

at 1 month old it was 75–80 per cent. This last value indicates that on 20–25 per cent. of the occasions at 1 month old, the pigs made wrong choices, a figure which may be compared with the corresponding one of 7 per cent. for the litter of Sow A. The earliest errors, it may be noted, have arisen largely from the fact that the pigs exchanged nipples more often than positions as the sow turned from one side to another. In most litters of about 1 month old, there is usually one pair of pigs, at least, which retain this early habit of exchanging nipples, e.g., Nos. 3 and 4 in Table 2.

The exceptionally large number of errors made by the pigs in this litter may be attributed to some, or all, of the following causes:

(*a*) The milk supply for this first litter of thirteen was inadequate, so that the pigs were often hungry, particularly when they reached three weeks of age. In this condition they were less inclined to insist on having the correct nipple.

(*b*) The litter eventually became so large in relation to the length of the udder that it was very difficult for a late-comer to insert itself into the right place even if it knew where it was.

(*c*) The presence of two pigs in the litter which often did not suckle (Nos. 11 and 13) provided opportunities for others to appropriate the spare nipples.

(*d*) The number of nipples was not the same on both sides of the sow, the fourth on the right being unpaired. The process of assorting themselves was therefore more complex for the pigs as the sow changed from one side to the other.

(*e*) Unlike sow A, sow C did not wait until all her pigs had found their proper places before letting down her milk, and thus encouraged them to trouble less about which nipple they were actually suckling.

These facts indicate that the chief means by which a pig finds its own nipple is by an appreciation of the conformation of the sow as a whole (in the sense of the *Gestalt* theory). To watch a litter of hungry pigs go through the process of suckling is to realize the remarkable accuracy with which they sort themselves out. There is no question of trying in various places until the right one is found. They go directly to the right place. This ability must be founded mainly on sight, with some capacity to recognize the feel of a nipple playing a secondary part. Hearing may be disregarded, and so may a sense of smell, for pigs placed with a foster mother will, if they are able, take up the positions they had on their original mother. An udder, moreover, which is coated with mud or some smelly substance does not appear to affect the positions of the pigs.

Another possibility, which does not seem to be important, is that the pigs may find their way by recognizing their neighbours. This clearly cannot apply to them all, and if the following short test of this possibility is generally valid, it does not apply to any. On four occasions, different pairs of pigs from the litter of Sow C which had been removed from their mother two hours previously, were put back with her before the remainder of the litter. Each time the pigs went directly to their own nipple and suckled, trying other nipples in a furtive manner when they realized they were not being used, and obviously keeping a watchful eye meanwhile on their own.

There is a peculiar habit, often exhibited, which may be of importance in orientating the pigs, although there is no reason to suppose that it is essential. This is the habit of communicating, snout to snout, with the sow before starting to suckle. A more probable explanation, which is also favoured by Shepperd [8], is that it is to encourage the sow to liberate her milk, especially since it occurs after suckling as well as before. A test in complete darkness should yield useful results.

Reviewed briefly, suckling preference in pigs arises very early in lif mainly from a desire to occupy always a particular position. Lat comes recognition of particular nipples. Departures from the norm distribution appear to be associated most commonly with large litte lack of uniformity in the udder, and certain kinds of maternal behavio In the first day or two the tendency to keep to the anterior glands of t udder is stronger than the desire to retain a particular position; but t inference that the pigs must be capable of estimating the milk yield fro the various nipples, and therefore 'choose' the anterior nipples, is n easily justified. A more probable explanation is that these nipples a in a much safer region, being farther away from the hind legs of the so Apart from this general tendency to move to the anterior part of t udder, little evidence has been found that young pigs 'choose' the nipples. The impression has been gained that the original distributi is largely due to chance, depending more on the times at which the pi begin to suckle at one nipple than on their relative weights. In gener nevertheless, the largest pigs will be found suckling the anterior nipple for, whatever their initial weight, they obtain most milk and will quick become the largest.

The variation in the weights of litter-mates, which has at tim interested various investigators, must for the present be regarded requiring little or no genetic explanation. Given mammary glands considerably different productivities, an efficiency in utilizing m which varies according to the quantity consumed [1], and a stro tendency for each pig to suckle at only one nipple, there may be no ne to postulate genetic differences in growth-rate. Although such diff ences probably exist, the observed variation must be mainly an effect inequalities in the milk-yield of the mammary glands of the udder. T problem then resolves itself into determining whether it is possible, selection, to remove these inequalities.

The Process of Suckling

Three distinct stages may be recognized. The first is a prelimin period during which the litter sorts itself out and stimulates the flow milk by massaging the udder. At this time also many of the pigs may round and touch the snout of the sow. Quite suddenly the second st begins during which the pigs suckle rapidly and do not massage. T third stage follows shortly and consists usually of an extended repeti of the first but includes rather more actual suckling. All stages are varying length; the third may extend to 15 minutes or more; on t other hand it may be practically eliminated. There is reason to beli that little or no milk is obtained during the third stage, for if the p are weighed immediately after the second, the increase is just as gr as it is when they have been allowed to remain for some time longer w the sow. On several occasions the pigs have been returned to the s for 15–20 minutes after removal at the end of the second stage, and w through what appeared to be the third stage. With one or two doub exceptions all the pigs lost weight slightly during this time. Whet

or not this result is pertinent to the question depends on whether suckling proceeds normally under such treatment.

The second stage was found to be shorter than might be expected. It is not always possible to secure a trustworthy measure of the time, but Sow A and her litter, referred to previously, behaved in a sufficiently regular and well-defined manner to provide a good estimate. The length of the second stage varied between 35 and 45 seconds, which means that the milk must have been liberated at a very rapid rate. On the average 50 grams of milk passed from each nipple in 40 seconds. As an average this may be comparatively high, but there must be many nipples which exceed it.

All the evidence available supports the view that some pressure mechanism must be responsible for the 'letting down of the milk'. It is in fact difficult to conceive so much milk being merely sucked through a soft collapsible tube in so short a time, and in any case, unless some stimulus is applied (except at or near farrowing) it is not possible to obtain more than a few drops of milk by hand. If a stimulus is applied either by rubbing the udder or by allowing one or two pigs of a litter to suckle, milk is easily obtained, and may often be seen to trickle from the more productive nipples. Hammond [9] has dealt at length with this subject and expands the theory that under stimulus an 'erection' of the udder occurs which provides the necessary pressure to force out the milk. Although the data now presented are not sufficiently critical to indicate whether or not there is a contemporaneous acceleration of the rate of secretion, the very short period of suckling, and the increased amount of milk obtained with increasing intervals between sucklings [1], are quite compatible with the erection theory alone.

Hammond's review also suggests that the significance of the third stage of suckling may lie in a changed composition of the milk which is withdrawn towards the end of suckling. It may be that the small quantities of milk obtained last are richer in fat and other milk constituents. Whether this is the explanation for the third stage or not, it is noteworthy that this stage is widespread in many kinds of animals, and does not appear to be merely an indication of unsatisfied hunger. Young pigs which have obviously had enough will go on suckling although the skin is stretched tight around them. Causal factors will no doubt be found to account for the frequency of suckling, the amount of milk secreted, the stages of suckling, and the varying composition of the milk.

Summary

The extent to which differences in the milk-yield of different mammary glands in the same udder will be reflected in varying weights of the litter-mates depends on the extent to which the latter confine themselves to suckling particular nipples. Data are presented which indicate that although strong preferences do exist among the members of a litter, they cannot always be satisfied. The chief factors influencing the number of departures from the normal distribution at suckling appear to be: (*a*) the number of pigs in the litter, (*b*) the suckling behaviour of

the sow, and (*c*) the uniformity (or lack of it) in the udder. It is sugges that during the first few days after farrowing the pigs become capa of recognizing their positions in relation to the conformation of the s as a whole, and that they later become accustomed to seeking the pro nipple in the upper or lower row as the sow changes from side to si The period during which the milk is 'let down' by the sow appear be very short (less than a minute), and it is concluded that all the obser tions made so far on the process of suckling can be well accounted for the 'erection theory'.

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THE RELATIVE IMPORTANCE OF SOW AND LITTER DURING THE GROWTH OF SUCKLING PIGS: A COMPARISON OF FOSTERED WITH NORMALLY REARED PIGS

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WITH the introduction of intensive methods of rearing pigs, and t development of highly fertile strains, the problem of combining p ductivity with effective control of mortality and unthriftiness has beco important. A recent report [1], giving details of the losses from th causes among young pigs, indicates that insufficient attention has b paid to this aspect of pig production. During the last six years, obser tions made on the Large White herd of the Institute of Animal Genet Edinburgh, lead to the conclusion that much morbidity proceeds fr inadequate nourishment of the suckling pig. Although errors of mana ment are no doubt frequently responsible for deaths, yet the fact that milk production of sows varies within wide limits suggests that, in ma cases, fertility may have outrun the capacity of sows for feeding th litters, which, in an under-nourished condition, become more suscepti to accidents and diseases.

Investigation of this subject is rendered difficult by the lack of suita techniques for estimating actual milk production. The weight of li alone is an indirect method open to various criticisms, but as a f criterion by which sows are to be judged, it has great value. Any mea therefore, by which it may be made to represent breeding-value m closely should improve the efficacy of selection.

The chief objections to the use of weaning or other weights of suckl pigs are, firstly, that they are too subject to environmental fluctuatio and secondly, that they are ambiguous in the sense that they do discriminate between the quality of the sows and their litters. Since milk production of sows cannot be readily measured, it is usually possible to determine whether differences in the growth of litter suckling pigs should be attributed to heredity or to milk supply. I previous paper it has been shown that considerable differences do e in the milk production of single nipples, and that these are associa with marked differences in the growth of the pigs attached to th nipples [2]. Information of this kind is too difficult to obtain for it t feasible to accumulate sufficient material for estimating the effects heredity, and a complementary line of investigation has therefore b carried on, which partially overcomes the objections to basing jud ments on weaning-weight. The method employed in this investi tion has been the exchange of pigs between pairs of sows farrowing approximately the same time in such a way that each sow reared a li of which half consisted of her own pigs and half the other sow's p The object of this report is to give a preliminary account of res

obtained. Up to the present the data are not extensive enough to justify either detailed statistical treatment or the drawing of far-reaching conclusions. What has been done by way of analysis is, however, sufficient to indicate that as an experimental technique, the exchange of half-litters can be of great value in the study of the growth of suckling pigs.

Method.—Provided the exchanging was effected during the 2nd to 4th days after farrowing, it was usually accomplished without much trouble. By this time the pigs had received the colostrum, but had not yet become strongly attached to their dam. It was not always feasible to ensure that the 'halves' were balanced in respect of either numbers, sex, weight, or age. If they were balanced at the beginning, losses by crushing, &c., sometimes unbalanced them, and it is possible that in some cases pigs were taken from a functional teat and forced to suckle one that had wholly or partially dried off. Objections on these grounds are met by assuming that the influence of sex and litter-size over the range involved is so small that the degree of unbalance existing may be neglected. Variation in age is necessarily slight and reflected in weight-differences which have been allowed for. Whether these assumptions are permissible is difficult to know, but as attempts to find out are usually defeated by the excessive variation from other causes, the question appears at present to be somewhat academic.

Nevertheless, in interpreting the results, the circumstances of the experiment should be borne in mind. It should be remembered also that during the first week of life there is a strong tendency for the largest pigs to attach themselves to the anterior nipples, which are usually the most productive, and that all the pigs tend to accustom themselves to suckling a particular nipple [3]. When an exchange is made after 4–7 days, the pigs which change their mother cannot find their usual places, and are obliged to accept a fresh nipple. If the fostered pigs are larger than the natural offspring, they succeed in occupying the best positions, if smaller they are forced to the rear. Weight appears to be the most important factor in determining this distribution of pigs along the udder. Whatever the initial weight, however, the weights of the pigs after 3 weeks or more of suckling are controlled principally by the productivity of the nipple which they have usually suckled.

In this experiment no data are available concerning the actual amounts of milk provided by the sows. It has to be assumed that, on the average, the fostered half obtained as much milk as the natural. This might not be justified if the fostered pigs had been appreciably smaller than the others and had been forced to suckle the less productive nipples. Since, however, the correlation between weight at time of exchange and weight at 3 weeks is only about +0·6 (see Table 4), it is clear that the largest pigs, during the first week, are only moderately successful in finding the most productive nipples. As there was a slight actual superiority in weight at the time of exchange of 0·16 lb. in favour of the fostered pigs with the paired sows, it seems reasonable to suppose that they were adequately compensated for the disadvantage of having to change their mother. In selecting pigs for exchanging, the main consideration was to make up litters as uniform in weight as possible.

For various reasons a number of litters were reared that were compos of pigs from two sows but were unaccompanied by other litters with corresponding halves. Data from these litters will be treated separat

Results.—As a first step in the analysis of the results, the aver weights of the pigs at three different times were obtained for each of various sub-groups. These weights, which are given in Table 1, sugg that, in comparison with the effect of initial weight, the effect of foste is in itself of no importance. It is conceivable, however, that a real eff might be obscured by the effects of initial weight, and further anal of the results to allow for this is made.

TABLE 1. *Average Weights at Time of Exchange and at 3 and 8 W old. Numbers of Animals in brackets.* A *sows farrowed before* B *sow*

	Exchange		*3 weeks*		*8 weeks*	
	Own	*Fostered*	*Own*	*Fostered*	*Own*	*Foste*
Unpaired sows (8) . .	2·7 (36)	2·6 (32)	9·1 (36)	8·2 (32)	23·4 (31)	19·4
Paired sows A (10)*. .	3·6 (43)	3·1 (51)	10·5 (43)	9·5 (51)	25·4 (34)	25·1
,, ,, B (10) . .	2·8 (51)	3·6 (42)	8·2 (51)	9·8 (42)	22·4 (35)	27·3
Total . .	3·0 (130)	3·1 (125)	9·2 (130)	9·3 (125)	23·7 (100)	24·2

* Only 7 pairs available at 8 weeks.

It is required to know whether the variation in quantity of the so milk accounts for all the observed variation in the growth of the litt or whether there is some variation between litters as born that is accounted for by differing environments in so far as those are conditio by the sows. The litters as reared should provide an estimate of va tion due to environment peculiar to each sow (including her milk), since the litters as born were reared as 'halves' in different environme their comparison should yield an estimate of the variation due eithe congenital causes or to common environment during the time from b to transfer (usually 2–4 days).

TABLE 2. *Mean Weights at Time of Exchange and at 3 Weeks with Nu of Animals in each Half-litter*

Sow A						*Sow B*					
Own (A)			*Fostered (B)*			*Own (B)*			*Fostered (A)*		
n	*Exchange*	*3 weeks*	*n*	*Exchange*	*3 weeks*	*n*	*Exchange*	*3 weeks*	*n*	*Exchange*	*3*
7	3·7	10·6	5	3·8	9·3	6	4·2	10·5	5	3·7	
2	3·8	12·4	5	4·0	10·1	3	3·5	11·2	4	4·0	
4	2·9	11·2	4	2·4	10·0	6	2·2	9·9	4	2·8	
7	4·1	11·8	5	3·3	10·2	6	2·4	5·9	4	3·8	
4	5·3	10·5	3	3·4	6·9	6	2·9	6·3	4	5·6	
2	3·1	12·0	6	2·1	11·8	4	2·3	7·8	4	2·8	
3	2·4	8·5	4	2·5	11·2	6	2·8	11·8	4	2·1	
4	3·2	9·5	8	2·5	7·2	4	1·9	3·7	3	2·9	
5	5·5	10·1	5	4·2	8·8	6	3·1	6·4	4	5·5	
5	2·3	7·9	6	2·8	9·2	4	2·9	8·6	6	2·4	
Total 36·3		104·5		31·0	94·7		28·2	82·1		35·6	

The statistical method adopted has been to calculate first the ave initial and 3-week weights for each 'half'-litter (Table 2), and the analyse the variance and covariance of the differences and sum an from them (Table 3). Since it was not possible to arrange that

half-litter should be of equal numbers, it has been thought best to use their mean weights. This avoids the complications of unequal numbers but involves the assumption that size of litter makes no difference to the weight-increase. Such an assumption is unlikely to be true if large litters were to be compared with small, but if, as here, litters are considered in pairs of similar size (except the eighth pair in Table 2), the influence of litter-size may be regarded as immaterial. From the differences given in Table 3, it seems unlikely that fostering has had any ill effects, but there has apparently been a tendency for Sow A to rear better pigs than Sow B, and for the litter farrowed by Sow A to do better

TABLE 3. *Mean Differences and Sum from Table 2*

Sow A—Sow B		*Own—Fostered*		*Litter A—B*		*A+B*	
Exchange	*3 weeks*	*Exchange*	*3 weeks*	*Exchange*	*3 weeks*	*Exchange*	*3 weeks*
−0·4	−0·1	+0·4	+2·3	−0·6	+0·3	15·4	39·9
+0·3	−0·7	−0·7	+1·5	+0·3	+3·1	15·3	45·7
+0·3	−0·9	−1·6	−1·1	+1·1	+3·5	10·3	43·3
+1·2	+5·9	−0·6	−2·7	+2·2	+5·9	13·6	38·1
+0·2	+0·9	−0·8	−0·3	+4·6	+7·5	17·2	33·9
+0·1	+6·5	+0·5	−1·5	+1·5	+1·9	10·3	41·1
0·0	−0·1	+0·6	+1·1	−0·8	−6·5	9·8	39·5
+0·9	+5·1	−0·3	−1·9	+1·7	+6·5	10·5	28·3
+1·1	+3·1	−1·1	−1·7	+3·7	+4·3	18·3	34·7
−0·2	−0·8	0·0	−2·0	−1·0	−0·6	10·4	35·0
Total +3·5	+18·9	−2·1	−6·3	+12·7	+25·9	131·1	379·5

than the litter of Sow B. Both sets of comparisons, however, are still complicated by the effects of weight at time of exchange. By analysing the variance and covariance of the data in Table 3, it is possible to eliminate from the comparisons the influence of initial weight, and at the same time to compare the variance of the three differences and the sum. These variances may also be compared with an estimate of the variance of the means of half-litters regarded as a measure of random error.

An analysis of variance on these lines is given in Table 4. It will be observed that in the first and second lines no mean has been taken out, since there is no reason to suppose that A sows and litters are different from B sows and litters, and the degrees of freedom are therefore 10. In this way a test is made of the null hypothesis that the differences between sows (i.e. litters as reared) and litters as born do not vary significantly from zero when compared with the error variance.

In preparing the estimate of error, Yates' method [4] has been used, in which allowance is made for unequal numbers in the half-litters by multiplying the sum of the variances within the half-litters by the sum of the reciprocals of the numbers in each half-litter. In the present instance the sum of the reciprocals amounted to 0·23485, which is to be multiplied by 4, giving 0·9394, since each entry in Table 3 is made up of 4 values from Table 2.

With the removal of the variance due to regression of final on initial weight, there has been a considerable reduction of the mean square in all the lines except the fourth. Even so, the remaining variance is large enough in the Sow A—Sow B, Litter A—Litter B, and A+B lines to be significantly greater than that occurring in the half-litters. Given an

error variance of 2·047, and n_1 and n_2 equal to 8 and 150 respectively the minimum mean square for significance at the 5 per cent. point is abou 4·1, and at the 1 per cent. point about 5·3. The evidence thus indicate that the differences between litters as born and as reared, and betwee pairs of litters, are too large to be accounted for in terms of the estimate error variance. The superiority of the fostered pigs, on the other hand is well within the limits of error.

TABLE 4. *Analysis of Variance of 3 Weeks' Weights adjusted for Weig at the Time of Exchange*

	D.F.	$(Init.)^2$	*Init.* × *Final*	$(Final)^2$	*D.F.*	*Sums of squares*	*Mean square*	
Sow A—Sow B . .	10	3·89	15·63	115·45	1	62·80	..	
					9	52·65	5·85	SS
Litter A—Litter B . .	10	48·13	87·69	219·97	1	159·77	..	
					9	60·20	6·69	SS
Own—fostered:								
Within . . .	9	3·13	3·97	26·12	1	5·03	..	
Mean	1	0·44	1·32	3·97	8	21·09	2·64	NS
					1	0·63	..	
A+B	9	94·85	−7·76	233·62	8	232·99	29·12	SS
					1	189·03	..	
Within half-litters . .	147	39·72	86·65	487·89	146	298·86	2·047	
			r (within half-litters) + 0·62					

NS. = non-significant; SS. = significant at 1 per cent. point.

The coefficients of regression of 3-week on initial weight calculat from each line are as follows:

Sow A—Sow B . . .	+4·018±1·23
Litter A—Litter B . . .	+1·822±0·37
Own—fostered . . .	+1·268±0·92
A+B	−0·082±0·55
Within half-litters . . .	+2·182±0·227

With the exception of the regression derived from the A+B column Table 3, they agree in showing the importance of initial weight on fi weight. Since the four positive coefficients are not significantly differe a further test of the significance of the sow- and litter-differences c be made using combined estimates of the regression variance in t manner shown in Table 5. Here the estimate of regression varian from the half-litters is combined with the estimate from the sow- a litter-differences separately. Whether it is in order to use an estim from intra-sow data to adjust inter-sow comparisons may be doubte the correct procedure would presumably depend on the extent to whi the factors determining the regressions were the same within and b tween litters. In so far as the regression within litters depends on t fact that a light pig has naturally a slower growth-rate than a heavier p it is likely to correspond with the regression arising from inter-s differences, but actually it is probably affected considerably by co petition among litter-mates for the anterior nipples. Whichever es mate of the regression is used, it may be concluded that, from time exchange until 3 weeks after farrowing, under the conditions of t experiment, real differences have been introduced by the sows in respe of milking capacity, and by the litters as born in respect of ability grow.

The absence of a regression between the sums of the pairs of litter means is somewhat unexpected. The explanation is possibly that seasonal or other factors affecting both sows of a pair equally have modified 3-week weight independently of initial weight, although this weight retains an influence which can still be measured by intra-pair comparisons. That there was a great deal of variation from one pair of sows to another in the mean 3-week weight of their litters is shown by the A+B line of Table 4. A large mean square in this line is to be expected, because seasonal and genetical differences between the pairs are combined. It does not appear possible, unfortunately, to arrive at a direct evaluation of the relative importance of environment and heredity, since each source of variation may contain the influence of both. The

TABLE 5. *Further Test of Significance of Sow A—Sow B and Litter A—Litter B Differences*

	D.F.	$(Init.)^2$	*Init.* × *Final*	$(Final)^2$	*Residual sum of squares*	*Mean square*
Sow A—Sow B+within half-litters	157	43·61	+102·30	603·34	363·37	
Subtract residual sum of squares for half-litters alone . . .	147	..	..	..	298·85	
Sow A—Sow B	10	..	..	..	64·52	6·452
Litter A—Litter B+within half-litters	157	87·86	+174·36	707·36	361·34	
Subtract residual sum of squares for half-litters alone . . .	147	..	..	..	298·85	
Litter A—Litter B . . .	10	..	..	..	62·49	6·249

sow comparisons, for instance, have not been freed of age-differences, nor of the effects of previous history, such as size of previous litters (which may have affected udder-development), and they are hardly worth further consideration. The litter-differences, on the other hand, having been adjusted for initial weight, might be justifiably regarded as genetic in origin; but even here it is possible that something may have happened to the pigs *in utero*, or during the first few days on their own mother, which may have affected their later growth.

Analysis of the 8-week weights.—Between the ages of 3 weeks and 8 weeks the growth of suckling pigs outruns the available milk supply, which is supplemented by solid food in increasing quantities. The amount of milk consumed at 8 weeks of age is nevertheless in the neighbourhood of 40 per cent. of the total food consumption [5], and it may be safely assumed that the milk production of sows is important at all ages of the suckling pig. Thus variation in the average weight of litters at 8 weeks may be readily accounted for by differences in milk production, and although food is only one item in the environment peculiar to each litter as reared, the available evidence suggests that it is the most important item. As the experimental results under discussion were obtained with pairs of litters kept under conditions as similar as possible with separate penning and standard feeding, the observed differences between average weaning-weights may be even more properly attributed to variation in milk production. The significance and importance of these differences may be judged from the Sow A—Sow B line of Table 6, which has been constructed in the same way as Table 4,

although unfortunately only 14 sows are available for comparisons at th later age.

It is noteworthy that the variance of the A+B line has become small than that of the Sow A—Sow B line, although still significant at th 1 per cent. point. This could be explained by either a lessening of th effect of seasonal influences on the pairs of litters when milk is bein supplemented by meal, or more probably by an exaggeration of th differences between sows, because the first litter (as reared) to eat sol food will draw rapidly away from the other until it also starts troug feeding. Thus relatively small differences between sows at 3 week might become much larger at 8 weeks if no further differences are between them. Judged by the present data, the elimination of the effe of weight at 3 weeks on the final weight at 8 weeks shows that milk pr duction up to 3 weeks does have a considerable influence on the 8-we weights (see Table 7). The differences Litter A—Litter B are no long significant, but in view of the small numbers and the large error varianc the possibility that real differences do exist cannot be disregarded. Th effect of fostering is again shown to be negligible.

TABLE 6. *Analysis of Variance of 8-week Weights adjusted for Weight Time of Exchange*

	D.F.	(Init.)²	Init. × Final	(Final)²	D.F.	Sums of squares	Mean square	
Sow A—Sow B . .	7	1·93	+12·19	727·20	1	76·99	..	
					6	650·21	108·37	S
Litter A—Litter B . .	7	29·81	+134·55	791·44	1	607·30	..	
					6	184·14	30·69	N
Own—fostered:								
Within . . .	6	1·61	−8·49	59·15	1	44·77	..	
Mean	1	0·24	+2·12	18·57	5	14·38	2·88	N
A+B	6	45·32	−77·56	478·63	1	132·74	..	
					5	345·89	69·18	S
Within half-litters . .	97	32·73	+94·80	2,212·95	1	274·58	..	
					96	1,938·37	20·19	
			r (within half-litters) + 0·35					

NS. = non-significant; SS. = significant at 1 per cent. point.

As judged by the regression variances of Table 6, the weight at tim of exchange is still responsible for a considerable amount of variation individual weight at 8 weeks. Adopting the criterion that with an err variance of 20·19 any regression variance over 80 is significant at t 5 per cent. point, it will be seen that within half-litters and between t mean differences of Litter A and Litter B, initial weight maintains significant degree of importance. In the Sow A—Sow B line, howev it is no longer significant; and in the Own—Fostered line it remains i significant. The sums of the pairs now show a negative covarian leading to a significant regression variance. Interpreted in the light experience, these findings must mean that where competition exists (e within litters), initial weight is important in determining distributi along the udder and therefore final weight, but where competition do not exist (e.g. between one sow and another, or between pairs of sow or where it is only partial (e.g. between Litter A and Litter B), t

degree of importance of initial weight depends on the correlation between it and milk supply. If light initial weight happens to be associated with heavy milk production, it will involve no disadvantage, except where there is competition. If the available milk is substantially the same for different litters, initial weight may be expected to influence final weight, even where there is no competition, merely because the heavier of two animals growing at the same relative growth-rate will remain the heavier. These considerations are presumed to account for the positive regressions observed previously of 3-week weight on initial weight, where competition has been absent or partial.

The 8-week weights may also be adjusted for variation in 3-week weights, and the importance of sow and litter considered independently of the latter. This has been done in Table 7, which is to be compared with Table 6. The sow-differences are still too great to be due to random variation, and are therefore suggestive of differences in milk production between 3 and 8 weeks after farrowing, although the effects of other uncontrolled environmental factors have still to be measured. Investigations of this kind are liable to be complicated by gradations of unthriftiness due to anaemia and other troubles which do not lend themselves to measurement. In general, they are likely to exaggerate real differences in milk production, since under-nourished animals are more prone to contract them.

TABLE 7. *Analysis of Variance, in which the Variance of the Final Weight at 8 Weeks is adjusted for the Initial Weight at 3 Weeks*

	D.F.	(Init.)²	Init. × Final	(Final)²	D.F.	Sums of squares	Mean square	
Sow A—Sow B . .	7	76·98	+151·19	727·20	1	296·94	..	..
					6	430·26	71·71	SS.
Litter A—Litter B .	7	109·18	+255·85	791·44	1	599·55	..	..
					6	191·89	31·98	NS.
Own—fostered:								
Mean . . .	1	1·12	+4·56	18·57	1	0·27	..	..
Within . . .	6	18·14	+2·23	59·15	5	58·88	11·78	NS.
A+B	6	111·60	+162·78	478·63	1	237·43	..	..
					5	241·20	48·24	S.
Within half-litters. .	97	373·65	+431·87	2,212·95	1	499·16	..	..
					96	1,713·79	17·85	..
			r (within half-litters) +0·47					

NS. =non-significant; S. and SS. = significant at 5 and 1 per cent. points.

No important alteration has occurred in the Litter A—Litter B, or the Own—Fostered lines. The mean squares in the remaining three of the five lines have been reduced as a result of increased dependence of 8-week weight on initial weight, in this case 3-week weight. Thus variations in 8-week weights are to some extent due to magnifications of differences existing 5 weeks previously. In terms of correlation coefficients calculated from the half-litter lines, the dependence alters from 0·35 for exchange and 8-week weights to 0·47 for 3- and 8-week weights. The small value of these figures indicates that even within the restricted conditions of individual litters, the passage of time is accompanied by considerable changes in the distribution among litter-mates of environmental factors favourable to growth.

As a further proof that fostering *per se* does not contribute a signific amount to the variability of litter-mates, the following figures deriv from eight unpaired sows may be presented. Litter and sow comparis are not possible and the value of the data lies only in the comparison fostered with naturally-reared litter-mates. As before, the mean diff ences of the two 'halves' have been squared and their products compu to provide the material for the adjusted estimate of the mean squa This last is to be compared with the corresponding error mean squa from half-litters (given in previous tables), which, although not deriv from the same information as the treatment mean squares, are consider to be better estimates of error variance. The treatment variance is ag less than the error variance.

TABLE 8. *Test of Significance of Differences arising between Fostered a Naturally-reared Suckling Pigs*

	D.F.	(*Init.*)² (*Exchange*)	*Init.* × *Final*	(*Final*)² (*3 weeks*)	D.F.	*Sums of squares*	*Me squa*
Own—fostered .	7	0·26	−0·30	9·85	1 6	0·35 9·50	.. 1·5
Error variance (from Table 4) .	..	..	..	..	146	..	2·0
		(Exchange)		(8 weeks)			
Own—fostered .	7	0·38	+5·70	154·25	1 6	85·50 68·75	.. 11
Error variance (from Table 6) .	..	..	..	..	96	..	20

Discussion

As shown in the preceding pages, the relative importance of sow a litter at any stage of suckling can be calculated without loss of essen information. According to the kind of information that is soug modifications in the method may easily be introduced. In the pres instance, it was merely desired to know what amount of variation weaning-weight might be attributed to sows and what to their litters, t intention being to investigate further that source of variation which w the most important under Shothead conditions. Under other conditio the results may be different, and it may be desirable to make compariso of breed and strain of suckling pig with sows controlled, or of seaso effects with heredity of sow and litter controlled. For these purpose would be necessary to select sows and litters for exchanging rather th to pair them quite at random as was done in this case. The distinct that has been made between Sow A and Sow B would then come to ha some meaning, and the variation of the pairs about their common me acquire a greater significance. Further, the exchanging might be e tended with advantage, the limit being reached when a group of, s 10 sows each reared one pig from each. From less complicated expe ments than this a very fair estimate of seasonal effects might be obtain from what would correspond to the A+B column of the foregoi Tables 3 and 4.

The results of the present restricted series of exchanges indicate that the most conspicuous feature has been the environment of the litter as reared, i.e. either milk production or other sow-conditioned influences have been of greater significance than any other source of variation. This is in accord with the previous findings from similar pigs [2], which indicated that the growth of suckling pigs was in close relation to the amount of milk they obtained. There is nothing unexpected about this result, but it is as well to be certain that any attempts to improve the development of pigs in the suckling stage should be properly directed. While attacking the problem from the dam's side, it should not be forgotten that evidence of litter-differences has been found in the 3-week weighings. These differences have the appearance of being hereditary, but more extensive material is desirable before finally accepting the present results. Whatever their cause, however, they were as important as sow-differences at 3 weeks, and although they produced no further significant effects between 3 and 8 weeks, the differences existing at 3 weeks had a very substantial influence on the 8-week weights. With the improvement which might be expected from the elimination of many of the poor-milking sows, litter-differences would acquire an enhanced importance.

Summary

The relative importance of sow and litter in determining the variation of the weight of suckling pigs has been investigated by means of paired litters farrowed at approximately the same time and divided each into two groups of pigs, one of which was left on its own mother, and the other transferred to the second sow in exchange for a similar group.

Preliminary results from twenty litters reared in this way indicate that in those litters an equal and significant amount of variation in the growth of the pigs up to 3 weeks was found between litters as born and litters as reared. A larger portion of the variation was produced by differences in the totals for each pair of mixed litters. This is attributed to a combination of genetical and seasonal causes.

The weight of the pigs at 8 weeks was found to be influenced considerably by the sow, but, when adjusted for variation in weight at 3 weeks, showed that the effect of litter as born was no longer significant.

Weight at time of exchange was found to affect both 3- and 8-week weights, the coefficients of correlation being 0·62 and 0·35. Between 3- and 8-week weights the correlation was 0·47. No ill effects from fostering could be detected under conditions in which the fostered pigs had equal chance with the naturally-reared litter-mates.

It is concluded that under Edinburgh conditions the most important factor in the growth of suckling pigs is the milk production of the sows. The significant differences between litters as born are suggestive of hereditary effects, but confirmation of this is desirable.

On the basis of the observed results, it is suggested that the exchanging of litters in some form would lead to useful results in a variety of investigations concerning suckling pigs.

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THE EFFECT OF PRENATAL WEIGHT-CHANGES IN BREEDING SOWS ON THE NUMBER AND SIZE OF NEW-BORN PIGS

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Introduction.—Emphasis has often been placed on the importance of securing litters of heavy pigs at farrowing. It is justified by the knowledge that the mortality among small pigs is higher than among large. The latter are better able to fend for themselves and suckle more strongly, although litters with a high average weight at birth do not necessarily grow faster than those with a lower average weight. Yet there seems to be remarkably little information as to how such heavier pigs are to be produced; is it a matter of feeding or breeding, or merely chance? Large and small pigs do occur in the same litter, and litters may consist on the whole of light or heavy pigs. To judge from the appearance of breeding sows in general, breeders appear to differ concerning the optimum weight at which to keep them, and any investigation of this subject is likely soon to encounter individual differences among sows with respect to the tendency to put on weight. In sheep it is known that the weight of a lamb at birth is affected considerably by the weight of the ewe, although there are many cases in which a ewe in poor condition will produce a large lamb and vice versa [1]. To what extent does this apply to breeding sows? Records of the breeding stock at the Edinburgh University Farm, Shothead, taken at regular intervals, provide a partial answer to this question, though the main object of collecting the records was that of elucidating the more general problem of assessing the factors affecting the weight and growth of young pigs in order to determine the effects of heredity. In the present paper attention is directed mainly to determining the effect of varying weight-increases in the breeding sows on the weight of the pigs born, distinguishing the effect on the average weight of the litter from the effect on the variability within the litter. The reason for this is that at present it is widely believed that the variability of the pigs within a litter is due to environmental differences in the uterus, and the question arises whether or not the raising of the general level of the nutrition of the developing embryos will tend to diminish these differences. This is an indirect method of examining the hypothesis that the size of pigs at birth is conditioned by the degree of success in the competition for space or nutriment during gestation [2]. If, as will appear, there are large differences in the average weight of litters when the weight-increase of the sows has been the same, then some inherent differences in the sows with regard to the giving of nourishment will be indicated.

Material and Methods

The data have been obtained from monthly weighings of all breeding animals in a Large White herd, together with their weight at mating, before and after farrowing, and at weaning. The little pigs were weighed

damp as they were born. A certain amount of approximation has be made in the records of a few of the sows which either farrowed bef they were expected to do so, and consequently missed the pre-farrow weighing, or could not be weighed immediately after farrowing. T weight-changes in the sows followed, however, a fairly regular cour and such approximations are probably a smaller source of error than necessarily single weighings. Further, the changes in sow-weight w which this paper is concerned are of such a size as to make the erro

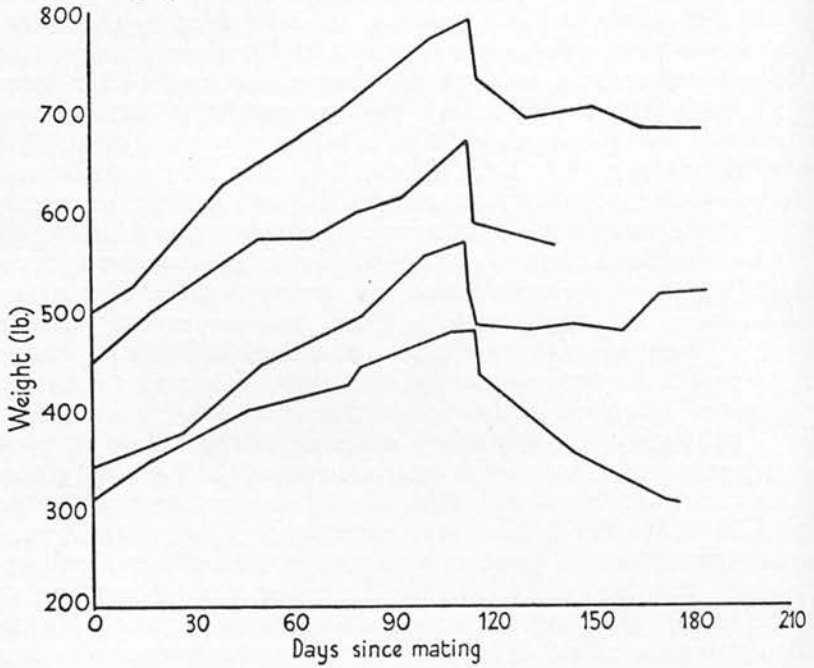


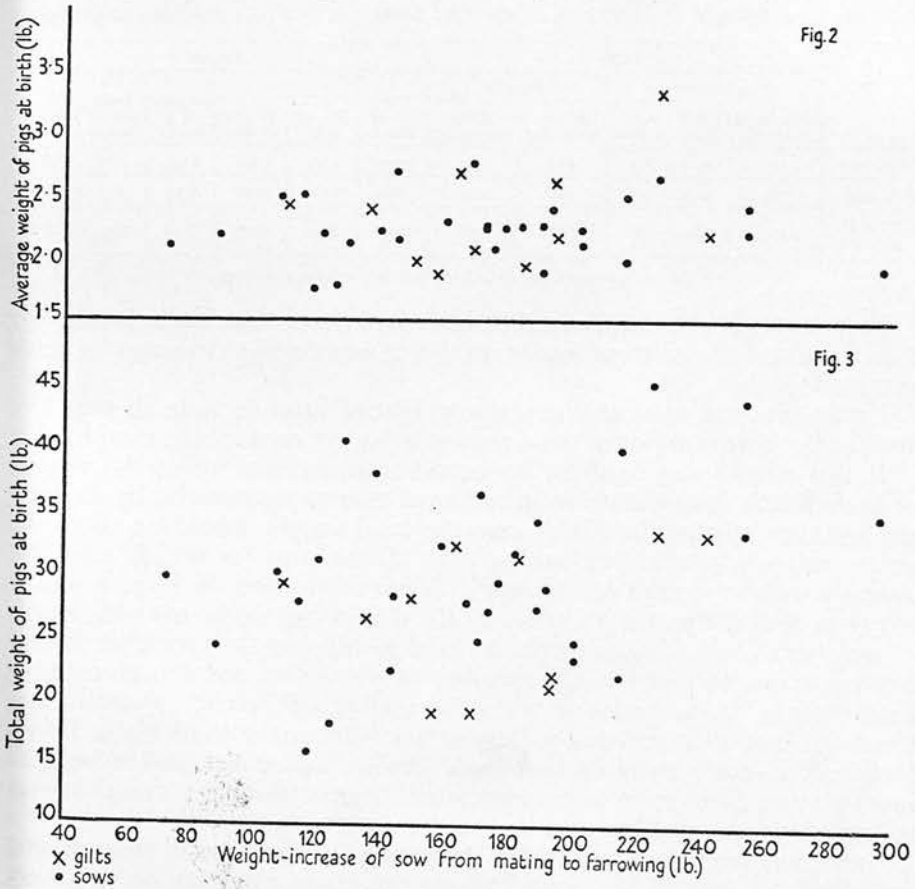
FIG. 1. Typical weight-changes in pregnant sows.

estimated or observed weight of comparatively slight significance. T weight-increases of the sows have been considered: (1) that from ma to just before farrowing; (2) that during the month prior to farrow (both (1) and (2) represent the weight-increase of the sow and developing litter); and (3) the weight-increase from mating to just farrowing, which may be said to represent the gain in weight of the herself during that period. The number of gestations involved is and the number of sows 23.

In an effort to increase the birth-weights, liberal to excessive feed was allowed. All animals were fed the same rations, but clearly did get the same quantities. This is to be concluded partly from observati of communal behaviour, and partly from the considerable differe in the weight-increases. All the sows put on at least 50 lb. betw mating and farrowing, so that the data to be presented do not directly with the effect of small increases or decreases. They are t distinguished, therefore, from those which are concerned with rat of varying quality [3, 4, 5, 6], or of defective composition [7, 8].

Results

Typical weight-changes are shown in Fig. 1. The rate of increase appears to have been fairly regular throughout the gestation period. The amount by which a sow loses weight after farrowing is conditioned greatly by her appetite as well as by the actual weight of the pigs born, plus placenta, &c. Many sows ate very sparingly after farrowing and lost weight rapidly until normal appetite returned. The distribution of the sows according to weight-increase can be seen by reference to Figs. 2 and 3. The ranges of increases covered by reasonable numbers are 100–230 lb. for the period from mating to just before farrowing, and 30–70 lb. for the month prior to farrowing.



FIGS. 2 and 3. Distribution of sows according to weight-increase.

The average weights and numbers of animals are given in Table 1. It was intended at first to separate the gilts from the older sows, but the data did not justify the separation (see also Figs. 2 and 3); nor did it justify the assumption that an immature gilt would compete with her litter for nutriment, and therefore exhibit a different relation between

the increase in weight of the mother and the weight of the litter from t exhibited by older sows. Both groups put on the same average incre during pregnancy, and the litter weights (allowing for fertility diff ences) were approximately the same. The correlation between num of pigs born and average weight per pig yielded a coefficient of −0· which, under the circumstances, is reasonably close to Axelsson's fig of −0·406 (1928). On the basis of the regression coefficient associa with the former value, it can be shown that if the gilts had produ 13·5 pigs per litter instead of 11·1, the total litter-weight would have b very close to that observed for the sows.

TABLE 1. *Average Weights of Sows and their Litters (all weights in pou*

	Dams					*Litters*					
	Weight-increase			*Weight*		*Total wt. of litter*	*No. of pigs*	*Av. wt. of pigs*	*Av. wt. at 3 weeks*	*Total wt. at 3 weeks*	
	Mating to farrowing	*Sow* alone*	*Last month*	*Before farrowing*	*After farrowing*						
Sows (30)	173	122	61	582	531	30·2	13·5	2·24	8·47	72·0	
Gilts (10)	169	126	48	446	403	26·0	11·1	2·36	8·55	76·9	
Sows and gilts (40)	172	123	58	548	498	29·1	12·9	2·27	8·44	73·2	

* Equivalent to weight after farrowing less weight at mating.

Sows and gilts thus appeared to have had more than enough food their own and their litters' needs, so that it was decided to consider t groups together.

Litter-size and total and average weight of litter include all pigs and dead. The number of dead pigs was 7·4 per cent. of the total bir

If the quantity of food fed to brood sows were to affect the we of their litters it might do so in either of two ways, namely, by alte the number of pigs (in which case the total weight would be affect or by altering the individual weights of the pigs (in which case average weight would be affected). Mere inspection of Figs. 2 an suggests that if there is an effect at all, it is rather slight over the ra of weights shown. Fig. 3 might be held to support the view that libe feeding tends to increase the number of pigs born and therefore t total weight, in accordance with the results of Zeller, Johnson, Craft [9], but with material no larger than that so far available in Ed burgh, it is quite possible that high fertility and considerable wei increase merely happen to be associated. Fig. 4 illustrates the obse relation between fertility and increase in sow-weight.

Attention may be drawn to the large range of variation in average total birth-weight. Figs. 2 and 3 show that sows putting on appr mately the same weight often produce litters differing by as much half a pound in average weight at birth, which is of the order of 20–25 cent. Similarly, differences of the order of 30–35 per cent. of the aver commonly occur in total weight of litter. Data appropriate to Figs and 3 are given in Table 2, which shows the amount by which the v ance of total and average birth-weight would be reduced if the incre in sow-weight from mating to farrowing could be held constant. P

tically no reduction would occur in respect of average birth-weight and only about 11 per cent. in respect of total weight.

A similar analysis has been made of the effect of the weight of the sow from the mating to farrowing on the three-week weight of the total litter. The weight-increase of the sows during the last month of pregnancy, their actual weight at farrowing, and the weight which they put on to themselves as distinct from their litters have been examined in relation to the total and average weight of the pigs at birth and their total weight at three weeks. The weight which the sows have been deemed to put on to themselves has been calculated by subtracting from the weight after farrowing the weight at mating (an adjustment for weight after farrowing having been made in a few cases). The results are summarized in Table 2.

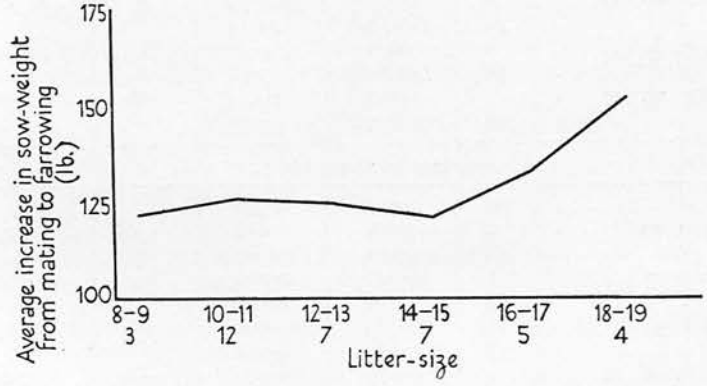


FIG. 4. Relation between litter-size and average increase in sow's own weight from mating until farrowing.

The conclusions indicated by the data in this table are that total birth-weight increased with increasing weight of the sow as measured both during the whole pregnancy and during the last month of it; and the total weight of the sow just before farrowing (including, therefore, the weight of the litter) had a similar relationship, but perhaps rather closer than that to be expected solely from the fact that her weight would obviously include the weight of the litter. As opposed to all this, the amount of weight which the sows themselves put on, that is the difference between their weights at mating and just after farrowing, failed to show any relation to the total weight of the litter. This suggests that the significant regression of total birth-weight on increase in sow-weight is due to the inclusion of the litter-weight itself in the latter. The principal conclusion so far, therefore, appears to be that there is at most only a slight connexion between total litter-weight and weight-increase of the sows. Different results would probably be found if the normal food requirements of sow and litter were not satisfied. Another clear fact is that the heaviest sows had the heaviest litters, but the importance of this statement is somewhat diminished by uncontrolled fertility differences and by the inclusion again of the weight of the litter itself.

That average birth-weight showed no relation to sow-weight or in crease in weight also tends to discount the results in the previou paragraph. There is, indeed, a significantly smaller variance due t regression than that to be expected from chance alone, for which ther

TABLE 2

A. Total birth-weight

Variance	*D.F.*	*Sum of squares*	*Mean square*	*Significance*	*Per cent. of total variance due to regressio*
Total	39	1796·40	46·06		
Due to regression on (1)	1	206·75	206·75	S	11·51
Remainder	38	1589·65	41·83		
Due to regression on (2)	1	185·43	185·43	S	10·32
Remainder	38	1610·97	42·39		
Due to regression on (3)	1	384·17	384·17	SS	21·39
Remainder	38	1412·23	37·16		
Due to regression on (4)	1	89·42	89·42	NS	4·98
Remainder	38	1706·98	44·92		
B. Average birth-weight					
Total	39	3·513	0·901		
Due to regression on (1)	1	0·044	0·044	NS	1·25
Remainder	38	3·469	0·091		
Due to regression on (2)	1	0·00035	0·00035	S*	0·01
Remainder	38	3·513	0·092		
Due to regression on (3)	1	0·026	0·026	NS	0·73
Remainder	38	3·487	0·092		
Due to regression on (4)	1	0·064	0·064	NS	1·82
Remainder	38	3·449	0·091		
C. Total weight at 3 weeks					
Total	35	33363·12	953·23		
Due to regression on (1)	1	765·34	765·34	NS	2·29
Remainder	34	32597·78	958·76		
Due to regression on (2)	1	20·45	20·45	NS	0·61
Remainder	34	33342·67	980·67		
Due to regression on (3)	1	1197·80	1197·80	NS	3·59
Remainder	34	32165·32	946·04		
Due to regression on (4)	1	919·46	919·46	NS	2·76
Remainder	34	32443·66	954·23		

* Significantly less than expected.
(1) Weight-increase of sows from mating to farrowing.
(2) Weight-increase of sows during last month of pregnancy.
(3) Total weight of sows at farrowing.
(4) Weight-increase of sows apart from litter from mating to farrowing.
S = significant over 5 per cent. point but below 1 per cent. point.
NS = non-significant. SS = significant over 1 per cent. point.

is probably no biological reason. Negative results were also obtained in relation to three-week weights, which have clearly been unconnected with the weight of the sow. In contrast to this result, Zeller, Johnson and Craft [9] found at Beltsville that the heavier sows at farrowing weaned more and heavier pigs.

In the last column of Table 2 is shown the amount of the variance in total birth-weight, or average birth-weight, or three-week weight, which would be eliminated when sow-weight or weight-increase was held constant. The amount is negligible except for total birth-weight, but it would not be safe to conclude that as much as 10–20 per cent. of the variance would be lost with another group of sows in the same weight-range but with a different relation between weight and fertility.

Relation between Sow-weight or Increase in Weight and Variability in Birth-weights

It is conceivable that if competition among litter-mates *in utero* were responsible for their variability in weight at birth, the provision of sufficient nutriment for the needs of all would decrease that variability. A comparison has therefore been made of the variability within each litter (reckoned as the mean square deviation) with certain of the sow-weights used previously. The method of correlation has been employed for the purpose and the coefficients obtained are given in Table 3.

TABLE 3. *Correlation Coefficients*

Intra-litter variance and	*Sows (30)*	*Gilts (10)*	*Sows and gilts (40)*
weight of sow after farrowing	−0·074	+0·251	+0·070
weight-increase of sow from mating until just after farrowing	−0·368	−0·014	−0·267

5 per cent. levels of significance [10] for r are 0·349, 0·576, and 0·304 for n equal to 30, 10, and 40 respectively.

Of the coefficients given, only one seems unlikely to be due to a chance association. If it measures a real correlation, then in the sow group an increase in the body-weight put on by the sow during pregnancy has been associated with a decrease in the variance of the litter. Whilst confirmation of this conclusion is desirable, it may perhaps be used in considering the relation of sow and litter *in utero* until more extensive data are available. With this reservation it may be concluded that the actual weight of the dam has little or no influence on the variability of the litter, but that her weight-increase may have some. Little importance can be attached to the value of the coefficient for weight-increase and litter-variance for gilts, owing to the small numbers.

Discussion

The salient fact emerging from this experiment is that the attempt to increase the weight of pigs at birth by liberal feeding of their dams has failed. The numbers of pigs per litter may have been increased slightly, but not their average weight. During their pregnancies the sows put on a great deal of weight, so that the capacity of their digestive organs to absorb nutriment is not the limiting factor in foetal development. If the possibility that a qualitative deficiency in the diet existed is disregarded, the absence of any marked relation between the weight the sows put on themselves and the weight of their litters indicates that

either the foetal pigs are unable to utilize fully the available food supply or they are limited in their growth by the mechanism for the nourishment of a litter *in utero*. The first alternative seems unlikely in view of the long time during which natural selection must have favoured those animals genetically best fitted for uterine growth, and of the occasional occurrence of whole litters of relatively large pigs. Lush, Hetzer, and Culbertson [11] attribute only 6 per cent. of the total variance in birth-weights of gilts' litters to heredity. The double-mating experiments of Carroll and Roberts [12], and of Shearer, Evvard, and Culbertson [13] also indicate that variation in birth-weights is but slightly affected by heredity.

The performances of gilts as compared with those of sows support the view that at the level of nutrition concerned there is no great difference in their relative abilities to nourish their young during pregnancy. It has been established by many investigators that the fertility of gilts is lower, and consequently the only difference between sows and gilts would appear to be in the numbers of eggs successfully implanted, and not in any immaturity of uterus.

The results obtained by Mohler [14] do not seem to be quite comparable with those now presented. He found that five small-type Poland-China sows averaged 4·2 pigs born, as compared with 6·7 pigs from eleven intermediate and large-type sows; sow-weight was associated with an effect on fertility, but the sows were, purposely, not homogeneous as were those used in our investigation; and thus genetic differences in either fertility or ability to nurture pigs *in utero* may be involved. If the latter alternative is correct, the Beltsville results may be regarded as evidence of the differences in uterine level of nutrition discussed above.

Summary

1. An attempt to increase the average weight of pigs at birth by liberal feeding of the dams during gestation failed. The amount of the variance in average weight per litter due to differences in (*a*) weight-increase from mating till just before farrowing, (*b*) weight-increase during the last month of pregnancy, (*c*) total weight of sow just before farrowing and (*d*) weight-increase of sow herself from mating till just after farrowing, was negligible.

2. Total birth-weight was not affected by the weight-increase of the sow herself during pregnancy.

3. Three-week weight of whole litters was not affected by either (*a*), (*b*), (*c*), or (*d*) above.

4. No relation between intra-litter variance in birth-weight and weight of sow after farrowing was observed. Sows considered apart from gilts showed a negative correlation (just significant at the 5 per cent. point) of −0·37 between weight-increase of sows from mating till just after farrowing and litter-variance in birth-weight.

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Sources of Variation in Human Birth Weights

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MCMXXXIX

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IX.—**Sources of Variation in Human Birth Weights.** — By **H. P. Donald,** Ph.D.(Edin.), Institute of Animal Genetics, University of Edinburgh. (With Three Graphs.)

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AT times when processes of great ontogenetic importance are taking place, the interaction of heredity and environment presents problems of considerable interest. Laying as it does the foundations of future independent existence, prenatal development must be the concern of all those interested in the mental and physical suitability of human beings for the environment in which they have to live. Owing to lack of information, pregnancy from the point of view of the fœtus has perforce been largely neglected by the physician and sociologist, but the need to remedy this defect in our knowledge had been clearly indicated by Hogben (1931). As an example of a field of research that would repay much attention, the work of Pearson (1914) and S. Hansen (1920) may be mentioned. These authors wrote suggestively of the handicap of the first-born, using extensive data on the incidence of disease, mental defect, and the physical qualities of the new-born child in relation to birth order.

According to the Registrar-General (1936), the greatest single cause of infant mortality is "premature birth," a fact which assumes great importance in days of falling fertility, and which brings human experience into line with that of animals, the survival of which is closely bound up with the weight and strength of the newly born. Both from the individual and the population aspect, therefore, it is desirable to know more of the intimate association of mother and fœtus. From the nature of its data, the investigation now reported emphasizes the inequality of mothers rather than the varying response of fœtuses to the uterine environment, but it is to be recognized that birth weight may not only be controlled by the characteristics of uterine environment, but also be subject to genetical influences arising from within the fœtus itself.

The background of knowledge for the investigator of human birth weights consists of some few papers dealing with actual human birth weights and a considerable number devoted to the birth weights of animals. Of the former, only that of Toverud (1933) need be mentioned here. This paper is chiefly concerned to establish the importance of the seasonal food variation, and of the mothers' social status on the nutri-

tional condition of the new-born. Evidence is quoted and figures given to support the idea that the diet and occupation of the mother affect the weight of the new-born, but the question whether this is due entirely to modification of the length of pregnancy is not settled. This is a difficulty that besets all workers with human material, since any factor affecting the birth weight may do so by altering either the gestation period or the growth rate or both. In the present report, the main interest centres around the relative importance of such factors as season of birth, sex, and family. It will be shown that whereas the first two are of minor importance, the influence of family is so strong as to preclude the possibility that it might be accounted for by slight changes in the duration of pregnancy.

For the purposes of this study, it is desirable to mention certain papers representative of many dealing with two other types of investigation which have an indirect bearing on the problem here discussed. There is firstly the evidence of the waves of growth in the organs and tissues of man during gestation (Jackson, 1909; Bean, 1924; Schultz, 1926) and the critical stages through which the embryo passes (Stockard, 1920). The facts presented by these and other authors lead inevitably to the question of the relations between birth weight, stage of development (the cerebellum and intestines, for instance, are growing strongly during the last month of pregnancy), and subsequent development after the check to growth at birth. The second type of investigation deals with genetical differences in birth weight observed in animals. Species and breed crosses have been frequently made and the effects of heredity demonstrated. In some cases a large effect is claimed (Chapman and Lush, 1932, in sheep) and sometimes only a small one (Lush and others, 1934, in pigs). The classical genetical analysis of birth weights is that of Wright (1922) in guinea-pigs. A reorientation of the whole problem has been given by the work of Walton and Hammond (1938), who have clearly shown the importance of "maternal control" with the aid of a wide outcross between Shire horses and Shetland ponies. Whichever way the cross was made, the resulting foal was of a size appropriate to the dam's breed, and was not intermediate. There is, therefore, a division of hereditary effects to be made—(*a*) those arising from the genetic constitution of the fœtus, and (*b*) those arising from the genetic constitution of the mother and determining the physiological standards of her pregnancy.

Material and Methods.

Through the courtesy of the authorities concerned, access has been obtained to records of the Elsie Inglis Memorial Maternity Hospital, Edinburgh. It has been possible to utilize a mere fraction of the data

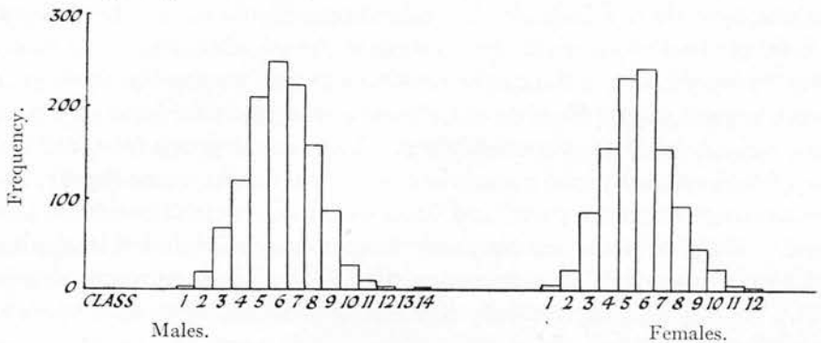
available, and there is a large fund of information waiting to be extracted from the detailed and well-kept records. Two main groups of birth weights have been collected: (*a*) individuals, (*b*) families. In the first, each weight has been classified according to the sex of the child, the month of birth, and the age of the mother at time of birth, for the last three years up to August 1938. Further sub-division was made to form groups of first-, second-, and later-born children. The second group (*b*) consists of cases where two or more records are available for the same family, and here also age of mother, sex, and date of birth of the children have been noted. Weights of the second group have also been included in the first and larger group, with the exception that no mother is represented twice in the later-born category, only the first available weight after the first birth being taken.

It is important to note that the data have been selected. Cases of maternal toxæmia, premature births when noted at time of delivery, and all still-births and abnormalities have been excluded. This is an important qualification since differing results obtained in separate investigations may be traced to the inclusion or otherwise of premature or post-mature births. Slight deviations from the usual term of pregnancy are difficult to detect, and consequently only cases where the term was considered to be more than a fortnight short have been excluded on account of prematurity.

Weight has been chosen in preference to length or the length-weight ratio as being more suitable for the measurement of variations in environment. Owing to the tendency for skeletal growth to proceed comparatively uniformly in spite of moderate environmental fluctuations, while the muscle and fat tissues respond more readily and act as a buffer protecting the vital parts from injurious fluctuations, weight should be a more sensitive indicator than length. On the same grounds, environmental effects which are detectable only with large numbers can hardly be important to the bulk of the children. Even in districts where poverty is marked, the size and growth of the children is not appreciably different from that in more prosperous areas (Paton and Findlay, 1926).

As an indication that the sample of records taken may be regarded as normally distributed about its mean, Graphs 1 and 2 have been drawn from the data on first-born males and females. Both distributions take the form of the normal curve, an observation which was made previously by Westergaard (1890). The females, however, showed a slight but significant positive skewness ($\sqrt{\beta_1}=0{\cdot}311\pm0{\cdot}076$), which may mean that too many light-weight infants have been rejected as premature. These facts are important in the statistical treatment of the data and in

the interpretation of its results. The statistical methods used are those of Fisher (1936).



GRAPH 1. GRAPH 2.

Class 1 4·5— 4·9 lb.
,, 6 7·0— 7·4 lb.
,, 14 11·0—11·4 lb.

GRAPHS 1 and 2.—Frequency distributions of weight at birth of first-born children.

SEASONAL CHANGES IN BIRTH WEIGHTS.

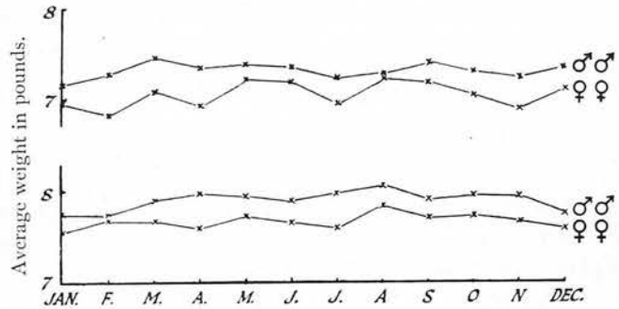
According to Toverud (1933), Norwegian mothers produced larger infants during late summer than at other times of the year, owing, she thinks, to the better supplies of fruit and vegetables. The extent to which this is true of Edinburgh can be judged from Table I, which shows the monthly averages for first- and second-born children, over a period of three years.

TABLE I.—SEASONAL CHANGES IN AVERAGE BIRTH WEIGHT (POUNDS).

Month.	First Born.				Second Born.			
	Males.		Females.		Males.		Females.	
	No.	Average.	No.	Average.	No.	Average.	No.	Average.
January .	98	7·17	89	6·96	35	7·33	34	7·41
February	85	7·30	74	6·82	31	7·57	40	7·17
March .	88	7·47	93	7·09	33	7·53	40	7·16
April .	115	7·37	95	6·95	30	7·78	23	7·75
May .	132	7·40	94	7·21	42	7·36	25	7·39
June .	90	7·36	99	7·22	26	7·39	24	7·60
July .	96	7·26	95	6·99	31	7·97	35	7·70
August .	88	7·30	93	7·23	43	7·44	29	7·57
September	91	7·41	85	7·20	30	7·67	29	7·55
October .	96	7·33	81	7·06	30	7·93	35	7·35
November	84	7·27	77	6·92	33	7·70	26	7·79
December	98	7·37	78	7·14	32	7·66	37	7·62
Totals .	1161	7·336	1053	7·073	396	7·60	377	7·48

Graph 3 shows these results in a more easily appreciated form. It suggests that among first-born children males are regularly heavier than females, and less affected by seasonal fluctuations in average weight.

The second-born children, owing to the fewer numbers, showed greater variability of average weight from month to month, and no clear difference in weight according to sex. These anticipations are borne out by



Above—Edinburgh data, first-born only.
Below—Oslo data (Toverud, 1933), all births.

GRAPH 3.—Seasonal distribution of average birth weight (in pounds) for Edinburgh and Oslo (Toverud).

the analysis of the monthly means in Table II. The three years' observations are treated separately for the first-born, but combined for the second-born children.

TABLE II.—ANALYSIS OF THE VARIANCE OF MEAN BIRTH WEIGHTS ACCORDING TO SEX, MONTH AND YEAR.

A. *First-born Children.*

Source of Variation.	D.F.	Sum of Squares.	Mean Square.	F.* Observed.	F.* 5 per cent. Point.	F.* 1 per cent. Point.
Sex . . .	1	1·254	1·254	47·7	4·0	7·1
Year . .	2	0·035	0·018	..	..	..
Month . .	11	0·611	0·056	2·1	2·0	2·6
Remainder .	57	1·497	0·026	..	..	..
Total . .	71	3·397	..	..	..	..

B. *Second-born Children.*

Sex . . .	1	0·069	0·069	2·3	4·8	..
Month . .	11	0·631	0·057	1·9	2·8	..
Remainder .	11	0·331	0·030	..	..	..
Total . .	23	1·031	..	..	..	..

* According to Snedecor (1934).

On these figures, sex and month of birth have an established effect on the weight of first-born children, but not year of birth. Neither sex nor month have a detectable effect on the means for the less numerous second-born.

Graph 3 shows that the influence of month of birth affects chiefly first-born females during the summer months May to September. The

anomalous fall in the average during July is due to an unexplained low average in one of the three years. Toverud's monthly averages show very little change except for a rise in August and a fall in December and January. Combining the evidence of both sets of data, it may be supposed that winter babies are sometimes slightly lighter and summer babies sometimes slightly heavier than the yearly average.

Effect of Age of Mother.

In the literature there is a certain amount of disagreement concerning the influence of age of mother on weight of offspring. Duncan (1871) and Toverud (1933) reported an association between the age of the mother and the weight of the child. H. J. Hansen (1913) and Heiberg (1911) hold the view that birth order and not age of mother accounts for the increasing weight of later babies. Neither factor is, of course, very useful as an explanation of why later babies are heavier. The present results are shown in Table III. They are confined to first and second births only, for which adequate numbers are available.

Table III.—Age of Mother, and Birth Weight.
(Number of births in brackets.)

Age of Mother.	First Born. Males.	First Born. Females.	Second Born. Males.	Second Born. Females.	Sex Ratio. First to Fifth Births. ♂♂ per 100 ♀♀.
15–19 *	7·27 (95)	6·95 (89)	7·55 (4)	7·20 (5)	106
20–24	7·35 (483)	7·05 (386)	7·65 (109)	7·39 (99)	122
25–29	7·31 (337)	7·11 (321)	7·65 (166)	7·54 (141)	108
30–34	7·34 (114)	6·94 (120)	7·47 (86)	7·60 (94)	95
35–42	7·56 (23)	7·24 (33)	7·44 (31)	7·22 (38)	72
All mothers	7·33 (1052)	7·05 (949)	7·60 (396)	7·48 (377)	108

* Including two mothers of 13 and 14 whose first female and male infants weighed each 6·5 lb.

So far as can be judged from the Edinburgh data, the weight of first-born children of either sex is not appreciably affected by the age of the mother. The weights of second children, on the other hand, show that both males and females increase in weight to a mother's age of about 25–30 years and then decrease again. This is in general agreement with the observations of Pearson, Duncan, and H. J. Hansen.

As a matter of interest, the sex ratio of children of mothers of different ages has been attached to Table II. The figures are hardly large enough to be of much value, but the occurrence of a low proportion of males at either end of the reproductive life of women has also been noticed by H. J. Hansen (1913). If it is true that, under good environmental conditions, the sex ratio rises, the low sex ratios must mean that the fœtuses of

the young and old mothers were exposed to more hazardous conditions than those of mothers of intermediate ages.

Influence of Time elapsing between Births on Birth Weight.

No reference to a previous examination of this possible influence has been seen. Yet if the growth of a fœtus depends on the supply of nutriment from the mother, it might be expected that the occurrence of a pregnancy immediately after a parturition and lactation would find the reserves of the mother at a low ebb to the detriment of the fœtus. There is some evidence bearing on this point from experiments with sheep, in which it was observed that breeding from immature animals resulted in retarded growth and development of both ewe and lamb (Griswold, 1930). It may be different in rodents. Cole and Hart (1938) found that in rats pregnancy stimulated growth, so that pregnant females were heavier than non-bred control females. Cattle, unlike other domestic animals, are expected to support a growing fœtus as well as to milk heavily during all but two months or less of a nine-month pregnancy.

For analysis of the differences in weight and time between pairs of children adjacent in the birth order, pairs of males and pairs of females have been chosen. Owing to the tendency usual in this type of data for values on either side of the mean to be associated with paired values which are closer to the mean (regression), differences between birth weights when the first is low are likely to be positive, whereas those between birth weights when the first is high are likely to be negative. In order to prevent this tendency obscuring the effect (if any) of the months between births, the first of the two births have been classified into five weight classes, a procedure which enables the effect of time between births to be estimated within each weight class for first births.

Table IV.—Time in Months (Time) and Difference in Weight (Diff.) between First and Second Births.

Weight of First Child.	Up to 5·9 lb.	6·0–6·9 lb.	7·0–7·9 lb.	8·0–8·9 lb.	9·0 lb. and over.	Total.
	Time. Diff.	Time. Diff.	Time. Diff.	Time. Diff.	Time. Diff.	Time. Diff.
Means—(1) Both males	35·1 +1·45	33·2 +0·48	32·9 +0·35	34·8 −0·32	36·6 −0·83	33·8 +0·21
(2) Both females	28·1 +1·07	31·7 +0·29	39·9 +0·17	33·2 −0·11	26·0 −0·43	34·7 +0·23
Number of families—						
(1) Both males .	8	34	57	36	8	143
(2) Both females .	7	34	38	9	4	92

Table IV provides a general picture of the situation and shows how the second births tend to be heavier than light first births, but lighter than heavy first births, the tendency over all births together, however, being slightly positive. The question whether time between births affects the weight of the second of a pair can now be answered from the analysis given in Table V, which follows the method of Fisher (1936).

TABLE V.—ANALYSIS OF VARIANCE AND COVARIANCE OF TIME IN MONTHS (TIME) AND DIFFERENCE IN WEIGHT (DIFF.) IN POUNDS BETWEEN SUCCESSIVE BIRTHS.

A. *Both Males.*

Source of Variation.	D.F.	(Time)².	(Time × Diff.).	(Diff.)².	D.F.	Regression Sum Squares.	Adjusted (Diff.)².	Mean Square.	F.* Observed.	F.* 1 per cent. Point.
Total .	142	44244	+ 88·1	113·1	1 141	0·18				
Within Wt. Classes.	138	44076	+129·4	78·5	1 137	0·38	112·9	0·80		
Between Wt. Classes.	4	168	− 41·3	34·6	1 3	10·15	78·1	0·57		
							24·4	8·14	14·28	3·92

B. *Both Females.*

Total .	91	35618	+139·2	63·4	1 90	0·54	62·9	0·70		
Within Wt. Classes.	87	33661	+169·6	55·4	1 86	0·85	54·5	0·63		
Between Wt. Classes.	4	1957	− 30·4	8·0	1 3	0·47	7·5	2·50	3·97	4·02

* See Snedecor (1934).

From this table it may be concluded that (1) the mean differences between births vary significantly according to the weight class of the first birth; in other words, there is a significant tendency for the second of a pair of births to be closer than the first to the mean of all births whenever the first has departed from that mean; (2) that an effect of months between births is not established by these data, since the regression sum of squares is not distinctly larger than the corresponding mean square; (3) that there is no relation between the time between births and the weight of the first of a pair. This conclusion can be derived from the first two columns of Table V. A further comparison of the differences in weight between first and third or fourth child in relation to the time elapsing between their births has led to similar results.

EFFECT OF ORDER OF BIRTH ON BIRTH WEIGHTS.

The extent of this effect has considerable importance from the fact that a relatively low birth weight among first-born children may have some connection with the mental and physical handicap of the first-born (Pearson, 1914; Hansen, S., 1920). Most investigators agree that there is an increase in weight up to the third child. What happens after that has not been satisfactorily determined owing to the inadequacy of the available numbers, but it seems likely that there is but slight change from the fourth onwards. A comparison of the results now presented with some previously obtained is afforded in Table VI. References to further data are given by Heiberg (1911).

TABLE VI.—EFFECT OF ORDER OF BIRTH ACCORDING TO VARIOUS INVESTIGATIONS.

Order of Birth.	1.	2.	3.	4.	5.	6.	7.	8.	9–10.	Total Number of Cases.
(1) Ingerslev, ♂♂ .	7·28	7·56	7·68	7·71	7·86					1833
Denmark, ♀♀ .	7·07	7·41	7·30	7·43	7·59					1617
(2) Hansen, ♂♂ .	7·74	8·10	8·34	8·32	8·49	8·47	8·45	8·43	8·49	3005
Denmark, ♀♀ .	7·49	7·80	7·94	8·14	7·95	7·98	8·16	8·07	8·05	2818
(3) Toverud, ♂♂ .	7·69 ←				8·16				→	2205
Norway, ♀♀ .	7·52 ←				7·88				→	2046
(4) Duncan, ♂♂ Scotland, ♀♀	7·20	7·31	7·35	7·19	7·45	7·32	7·31 (7 and over)			2087
(5) Pearson, ♂♂ .	7·01	7·36	7·41		7·70		7·91		7·59	856
England, ♀♀ .	6·76	7·08	7·33		7·36		7·32		7·65	866
(6) Donald, ♂♂ .	7·33	7·60	7·78	7·87						1571
Scotland, ♀♀ .	7·05	7·48	7·47	7·42						1465

All the data, with the exception of Hansen's, come from city populations. Hansen's were not collected at clinics, but by midwives in country districts. It is therefore difficult to judge whether the variations in average weight of the six series are attributable to the populations from which they were derived or to the methods of obtaining the data. The Norwegian and provincial Danish averages are, however, suggestive of real differences from the remaining city data. All the series agree in showing an increase in both sexes up to the third child. The males may thereafter show further slight increases, but it is not advisable to draw conclusions, because the numbers are small and because of the increasing proportion of births contributed by the poorer classes and parents of possibly sub-average physique.

It will be observed that all the data given in Table VI agree that the second-born female is slightly larger in general than the first-born male.

This permits an estimate of the importance of birth order as a source of variation in birth weight as compared with sex, namely, that the difference between first- and second-born children is equal to or slightly greater than that between males and females, but that after the second birth, birth order has a much smaller effect than sex.

Another point of interest (which has also been studied by Goldfeld, 1912) is whether the weight of females following males is different from that of females following females. The sources quoted in Table VI do not provide this information, so that only the present Edinburgh data can be given.

TABLE VII.—MEAN WEIGHTS OF FIRST- AND SECOND-BORN INFANTS (IN POUNDS).

	First.	Second.	Difference.	Number.
(1) Both males	7·471	7·655	+0·184 ± 0·113	143 pairs.
(2) Both females	7·072	7·338	+0·266 ± 0·130	92 ,,
(3) Male-female	7·461	7·539	+0·078 ± 0·127	119 ,,
(4) Female-male	7·146	7·645	+0·499 ± 0·115	100 ,,
(5) All males	7·466	7·651	+0·185 ± 0·081	262; 243 ,,
(6) All females	7·110	7·450	+0·340 ± 0·089	192; 211 ,,

Females following males are larger than females following females according to these means, but the difference (0·198±0·135) is not significant. Second-born males of both classes have practically the same mean weight. The change in uterine conditions responsible for the increased weight of second and later births is therefore largely independent of the sex and weight of the first fœtus.

SIMILARITY OF BIRTH WEIGHTS WITHIN FAMILIES.

Although obstetricians now commonly consider the birth weights as significant features of family histories, there appears to be little published evidence concerning the extent of the resemblance in birth weight of children of the same family. Apart from the obstetrical importance of such information, it is desirable for sociological reasons to know a great deal more of the relation between birth weight and subsequent mental and physical development, and of the extent to which birth weight is an individual and familial characteristic. For this latter problem, the family histories made available may serve as a preliminary source of information.

Since most of the families consist of only the first two children, they will be considered first. Such families can be naturally divided into four groups—male-male, male-female, female-male, and female-female. It has been thought well to deal with them separately, since both sex and order of birth have an established effect, at least on the first two births. Within these groups there was naturally much variation in birth weight,

which is measured by the total variance of Table VIII. This total variance has been subdivided into three portions representing the contributions due to (1) birth order and sex, (2) differences between the family averages, and (3) the remaining unknown causes of variation. Thus in the 454 families concerned, about 75 per cent. of the variation

TABLE VIII.—ANALYSIS OF VARIANCE IN FAMILIES OF TWO (FIRST TWO ONLY).

	Male-male.	Male-female.	Female-male.	Female-female.
Total variance	242·21	227·09	143·85	144·31
Variance between births (B)	2·42	0·27	12·45	3·27
Degrees of freedom	1	1	1	1
Mean square	2·42	0·27	12·45	3·27
Per cent. of total variance	1·00	0·12	8·65	2·27
Total variance less (B)	239·79	226·82	131·40	141·04
Degrees of freedom	284	236	198	182
Mean square	0·84	0·96	0·66	0·77
Variance between families	181·34	171·38	102·70	110·19
Degrees of freedom	142	118	99	91
Mean square	1·28	1·45	1·04	1·21
Per cent. of total variance	74·87	75·47	71·39	76·36
Remainder	58·45	55·44	28·70	30·85
Degrees of freedom	142	118	99	91
Mean square	0·41	0·47	0·29	0·34
Per cent. of total variance	24·13	24·41	19·95	21·38
Intra-class correlation	+0·51	+0·51	+0·56	+0·56

in birth weight arose from differences among the family averages instead of 50 per cent., which would be expected in families of two if there were no tendency for sibs to be more alike than non-sibs. Compared with this, the amount due to sex and order of birth (in which most previous investigators have been interested) is almost negligible. Where the children were of the same sex, birth order was responsible for only 1 per cent. (males) and 2·27 per cent. (females) of the total variance. The interaction of birth order and sex in the other two groups accounts for the lower and higher values (0·12 per cent. and 8·65 per cent.). The statistical significance of each controlled source of variation may be judged by comparing the mean squares derived for each with the error mean square obtained from the remainder variance within each of the four groups. In the families of two males, the mean square for differences due to birth order is 2·42 with one degree of freedom, which is to be compared with the error mean square of 0·41 with 142 degrees of freedom. According to Snedecor's method (1934), the ratio 2·42/0·41 = 5·9 is compared with the tabled value of 3·9 for the same degrees of freedom. The tabled value gives the lower limit of all values which would occur by chance only once in twenty samples, and since the observed value is

greater, the chance that the observed effect of birth order is merely an accident of sampling is less than 5 per cent. By the same process it may be shown that the effect of birth order in the families of two females and the combined effect of birth order and sex in the female-male families are also significant. In the male-female families the effects of sex and birth order cancel each other, so that the net effect on the variance is non-significant. Similarly, in each group, the mean squares between families give, with the corresponding error mean squares, a ratio of about 3, a value which exceeds the 1 per cent. point for the appropriate degrees of freedom, so that the effects of family may be considered very significant.

Similar calculations have been made for families of three and four children. From the discussion of birth order above, it will be expected that as the family becomes larger the significance of birth order will diminish, and indeed it can only be demonstrated in the large group of families of three of mixed sex, in which it cannot be easily separated from the influence of sex. In respect of family, however, what has been found true for families of two holds as strongly for families of three and four (Table IX).

TABLE IX.—THE SIGNIFICANCE OF BIRTH ORDER AND FAMILY IN FAMILIES OF THREE AND FOUR.

	Number.	Mean Square.			Significance.	
		Birth Order.	Family.	Error.	Birth Order.	Family.
Families of three—						
All males .	21	1·29	1·71	0·52	NS	SS
All females .	13	0·19	1·01	0·34	NS	S
Mixed sex .	82	1·80	2·11	0·42	S	SS
Families of four—						
Mixed sex .	35	0·14	2·61	0·54	NS	SS

NS, non-significant; S, significant at 5 per cent. point;
SS, significant at 1 per cent. point.

The resemblance between sibs accounting for the significance of family may be expressed in terms of an intra-class correlation (Fisher, 1936) calculated for Table VIII, by comparing the reduction in the value of the mean square due to eliminating the effects of family with the original value. In the male-male families this is $(0{\cdot}84 - 0{\cdot}41)/0{\cdot}84 = +0{\cdot}51$. The values obtained show that the environmental and genetical factors concerned occur in combinations which are as strongly characteristic of families as those determining, say, mature height. Comparison of the mean squares within families ("remainder" in Table VIII) and between families shows that the latter (and therefore the estimates of sib correlation) are strongly significant. This conclusion has been checked by

making similar calculations for other groups of children, namely, first and third, second and third, first and fourth, families of three and families of four. The correlations are given in Table X. Allowing for the variation in the coefficients owing to the smaller numbers of families, it will be seen that the estimate of sib resemblance is approximately 0·5. A combined estimate based on the independent combinations of Table X yields the value 0·48.

TABLE X.—INTRA-CLASS CORRELATIONS MEASURING FAMILY RESEMBLANCE IN BIRTH WEIGHT. VARIANCE DUE TO BIRTH ORDER AND SEX REMOVED UNLESS OTHERWISE STATED. NUMBERS OF PAIRS OR FAMILIES IN BRACKETS.

Independent Combinations.	Correlation Coefficient.	Derived Combinations.	Correlation Coefficient.
Families of two—		Two children—	
Male-male	0·51 (143)	(1) First and third:	
Male-female	0·51 (119)	Male-male	0·57 (35)
Female-male	0·56 (100)	Male-female	0·51 (35)
Female-female	0·56 (92)	Female-male	0·39 (33)
		Female-female	0·26 (32)
Families of three—			
Mixed sex	0·55 (82)	(2) Second and third:	
All males	0·44 (21)	Male-male	0·68 (52)
All females	0·40 (13)	Male-female	0·37 (45)
		Female-male	0·79 (48)
		Female-female	0·63 (46)
Familes of four—			
Mixed sex	0·49 (35)	(3) First and fourth, Second and fifth:	
		Sex disregarded	0·55 (35)

DISCUSSION.

The environmental and genetical characteristics of each family cannot, unfortunately, be completely separated. The only conjectures that may be made about their relative importance have to be based on the observed effects of those variations in environment which can be measured. These may be classed as external to both mother and child, for example, season of birth; and as internal to mother but external to child, for example, order of birth and age of the mother. None of these has an influence comparable with that of family. The only genetical difference which can be measured is that of sex, and here also the effect is relatively small. Bearing in mind the known ability of the fœtus in various mammalia to grow at the expense of the mother's own body weight, if necessary, it may be supposed that the mother may smoothe out the favourable and unfavourable impacts of environment. There remain the largely unaccounted for family differences which must, in the meantime, be attributed to the genetical constitution of the children and to the genetical constitution of their mother. The former determines the growth reactions

of the fœtuses to their uterine environment, whereas the latter determines the quality of that environment. The extent to which children are of similar weight at birth because they have grown in the same uterus cannot, as yet, be directly compared with the extent of their genetic similarity. Experiments with laboratory and domestic animals have established the influence of both "maternal control" (Walton and Hammond, 1938) and the genetical constitution of the offspring (Wright, 1922) in determining birth weight. Their relative importance varies according to circumstances, and the position in man is difficult to anticipate.

One characteristic of birth weights in general, the almost normal distribution of the weights, has a certain bearing on the matter. It may be supposed that if fœtal increases in size were subject to a law of diminishing response to increments of food supply, the distribution of weights at birth would show a skewness on account of a shortage of heavy births. This does not appear to be the case. The number of large babies is as great as would be expected on a purely random assortment of favourable genetic and environmental factors with additive interaction, and consequently it may be inferred that the capacity of the fœtus to grow is, in general, not limited by its own diminishing response to favourable changes in the environment. Unless there is a tendency for both kinds of factors to act in the same direction (which may well happen since mating is selective), average birth weight must fall short of the maximum which it might reach. Thus a maternally controlled uterine environment could be the limiting factor in respect of average birth weight.

On the other hand it is to be expected that a sib correlation of 0·5 would be found in a character exhibiting purely genetic variation. With random mating, half the genetic variation would occur within families, but the fact that the observed variation within families approaches this figure does not necessarily mean that such a character is involved. Furthermore, the interpretation of such estimates of family resemblance is rendered more difficult by the absence of information about the effects of sampling. When a fairly uniform social group is used as the basis of the calculations, as is the case here, the applicability of the results to the population as a whole depends on whether the intra-familial differences in other social groups are of the same order. For a discussion on this subject, Hogben (1933) should be consulted.

Evidence from identical and non-identical twins in respect of birth weight has to be regarded with caution, since the assumption that the fœtal nutrition of both classes is subject to essentially the same conditions may not be tenable. In the meantime, however, it may be considered significant that Essen-Möller (1930) finds no greater resemblance in birth

weight among one-egg twins than among two-egg twins, although there is a greater resemblance in length. This bears out the supposition that skeletal growth is less affected by environment than the fat and muscle tissues, the plasticity of which protects bone growth, and that the genetical constitution of the fœtuses has a lesser influence on the birth weight than the genetical constitution of the mother in so far as the latter affects fœtal nutrition.

It may be useful to withdraw, in conclusion, some distance from the immediate problem of variation in birth weight, and regard it in relation to more general problems. Not only for obstetrical reasons, but for considerations of mortality, fertility, and post-natal physical development, birth weight has an inherent value. It is not a direct and unequivocal measure of growth, but at present what is lost in meaning is counterbalanced by the accessibility and scope of the material. To a considerable degree, birth weight represents the nine-months growth of tissues and organs in a particular type of environment. Of the growth of man in general it is known that the rate of development of the various parts relative to the whole and the remaining parts undergoes very great changes with the passage of time (Schultz, 1926). Imposed on these changes are the three phases of growth with their maxima and minima (Bean, 1924). When a child is born, that is, when it makes the change-over suddenly to a new mode of nutrition and respiration, the event must therefore be considered in relation to the stage of development which it has reached, for it is clear that shock and check might have far-reaching consequences when birth interrupts a stage of rapid growth such as a fœtus of five pounds weight would be commencing. As there seems to be no reason at present to suppose that there is any sharp distinction between "normal" full-term infants and premature or immature infants, it seems reasonable to assume that some of the dangers of child-birth to the child gradually diminish as the birth weight increases, and that a part at least of the disadvantage of the premature child is shared by the full-term child in some degree determined by its weight. This consideration does not, of course, apply to those difficulties of parturition which are increased by weight and size, but to the capacity of the child to adjust itself to the new conditions. Thus if, as Capper (1928), Sunde (1930), and Brander (1938) maintain on the basis of their extensive investigations, obviously premature and immature infants are subject to a heavy mortality, are on the average subnormal mentally and physically, and are more prone to nervous and respiratory disorders, it would not be surprising if these characteristics became less marked as the average birth weight for the population as a whole were approached and exceeded. For the same reason it is prob-

ably worth while investigating the physical and mental development of those families in which low birth weights occur regularly, since they may conceivably contribute more than their share of those unfortunates who are obliged to accept the hospitality of the State.

Summary.

1. An examination has been made of the factors affecting the birth weight of rather more than 3000 infants born at term of healthy mothers. The frequency distributions of the weights of first-born males and females showed a close approximation to normal curves (Graphs 1 and 2).

2. Monthly average weights show small but significant differences, tending to be higher in summer than in winter (Table II, Graph 3).

3. The effect of sex on birth weight is greater than that of month of birth, is about the same as that of birth order in small families, but accounts for comparatively little of the total variation (Tables II and VIII).

4. Age of mother had no apparent effect on the weight of first-born children, but may have had a slight influence on second-born children, mothers about thirty years old having the heaviest (Table III).

5. The time elapsing between births had no demonstrable influence on birth weight (Tables IV and V).

6. Data from six investigations, including the one now reported, agree that both sexes show an increase in weight up to the third child. The averages for later children are not consistent (Table VI).

7. Analysis of the observed total variation in birth weight indicates that whereas sex and birth order acting in the same direction cause less than 10 per cent., and much less when acting in opposite directions, differences between families of four or fewer children account for at least half the variation (Table VIII).

8. It is not possible with these data to determine directly how far birth weight as a family characteristic is dependent on the similarity of genetic constitution of the sibs as opposed to the constancy of their prenatal environment, but from various considerations the view is favoured that birth weight is a quality of the mother rather than of the children.

9. The significance of birth weight in relation to subsequent mental and physical development is briefly discussed.

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WEANING WEIGHT OF PIGS AND LITTER SAMPLING WITH REFERENCE TO LITTER SIZE

BY

A. D. BUCHANAN SMITH AND H. P. DONALD

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WEANING WEIGHT OF PIGS AND LITTER SAMPLING WITH REFERENCE TO LITTER SIZE

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(With One Text-figure)

INTRODUCTION

THE first part of this paper is concerned chiefly with the relation between weaning weight and litter size. It has been maintained that the average weight per pig at weaning is independent of the size of the litter (*Bull. N.Z. Dep. sci. industr. Res.*, 1930; Blissett, 1932; McMeekan, 1936). Average weights per pig given by Wild (1927) also show little variation with litter size. As against this, Murray (1934) presented data showing a decrease in weight per pig at 8 weeks as litter size increased. From their work on Mangalitza pigs, Contescu & Roman (1935) conclude that the weight of the whole litter is not proportional to the number of pigs in it and therefore the average weight per pig cannot remain unaffected by litter size. Further, Johansson (1931) finds that at 3 weeks there is a decrease in weight per pig as litter size increases, and this fact, taken in conjunction with the high correlations observed by Axelsson (1933) and Kronacher & Hundsdorfer (1936) between weights at 3 and 8 weeks, renders it doubtful whether the relation between litter size and weaning weight can yet be expressed in simple terms which are generally applicable. In view of the existing differences of opinion, the records of the past five years of a herd of Large White pigs maintained by the Institute of Animal Genetics, Edinburgh, have been examined with respect to the point at issue.

The second part deals principally with the associated question of litter sampling for the purposes of litter testing. With the exception of some investigations by Lush (1936), which will be mentioned in more detail later, there appears to be very little information available about this matter. Although the size of sample which can be dealt with by testing stations is affected by economic considerations, it is nevertheless as well to know something of the degree to which various types of sample can

represent the litter from which they are drawn, and an attempt has been made to supply some of the needed information. Underlying both these questions are fundamental problems concerning the growth of a litter, and it seems that until these have yielded to further study the selection of breeding stock at, or before, weaning must necessarily be carried out without much reference to genetic values.

Analysis of weaning weights

The majority of the litters were weaned and weighed exactly 8 weeks after birth; the weights of the remainder have been subjected to the necessary small corrections to make them comparable. The records date from 1931, and the management of the sows immediately before and after farrowing, and of the young pigs, has been uniform throughout. Within a year of starting the work it was considered that litters might be affected by differential treatment of the sows prior and subsequent to conception. Accordingly, since May 1932, all the sows have been treated similarly, and have received the same feeding before, as well as after, farrowing. Apart from ensuring access to the sows' ration, no attempt has been made to encourage litters with supplementary creep feeding.

For the purposes of the analyses, the average weaning weight has been calculated for each litter from the weights of the pigs alive at weaning, and the averages have been grouped according to the number of pigs in the litter.

Since it has been shown by Johansson (1931), Kříženecký (1935), and others that the age of the sow has an influence on the weight of the litter, the average weights obtained have been further subdivided into four classes based on litter sequence. Table I gives the condensed weaning weight data.

Table I. *Average weight in pounds per pig alive at weaning (with the number of litters from which the averages were obtained)*

Litter no.	Litter size									
	4	5	6	7	8	9	10	11	12	15
1	30·55	29·96	29·08	26·02	25·81	23·36	24·42	23·1	21·8	—
	4	3	4	5	8	5	5	2	1	—
2	—	—	33·3	26·32	28·33	27·92	28·1	28·57	26·53	19·3
	—	—	2	5	4	6	4	3	3	1
3	36·8	—	—	29·5	34·0	27·8	30·47	28·53	22·3	—
	1	—	—	2	2	7	3	3	2	—
4–9	—	36·7	29·55	30·1	26·05	29·93	28·03	31·0	22·96	—
	—	1	2	4	2	7	3	1	5	—

Inspection of this table shows that the average litter weight of gilts' litters is below that of older sows. There is also a fairly well-defined difference in the average weight of large and small litters, although within the range of litter sizes 7–11 the average weight seems to remain fairly constant for sows which have had one or more litters. The averages for gilts show a gradual reduction in average weight throughout the range. On the assumption that a simple linear regression of weight on litter size exists, an analysis of the variance of these weights has been made and is given in Table II.

Table II. *Analysis of variance in litter weights*

Variance	D.F.	Sum of squares	Mean square	S.D.	Log S.D.	z
		First litter				
Regression	1	205·60	205·60	14·339	2·663	0·984*
Deviations	7	22·23	3·18	1·783	0·578	−1·101†
Within classes	28	804·94	28·75	5·362	1·679	—
Total	36	1032·77	28·69	—	—	—
		Second litter				
Regression	1	48·69	48·69	6·978	1·943	0·475 N.S.
Deviations	6	102·98	17·16	4·142	1·421	−0·047 N.S.
Within classes	20	376·94	18·85	4·342	1·468	—
Total	27	528·61	19·58	—	—	—
		Third litter				
Regression	1	119·47	119·47	10·931	2·392	0·597 N.S.
Deviations	5	98·58	19·72	4·441	1·491	−0·304 N.S.
Within classes	13	471·67	36·28	6·023	1·795	—
Total	19	689·72	36·30	—	—	—
		Fourth–ninth litters				
Regression	1	153·87	153·87	12·406	2·519	1·326*
Deviations	6	111·60	18·60	4·313	1·462	0·269 N.S.
Within classes	17	184·81	10·87	3·297	1·193	—
Total	24	450·28	18·76	—	—	—

* $P>5\%$. † $P>1\%$. N.S. = non-significant.

The coefficients of regression are: (1) −1·111, (2) −0·637, (3) −1·333, (4) −1·216, and the analysis shows that the first and the last are significant. The standard errors of the other two are less than the coefficients, so that there appears to be a significant regression of weight on litter size equivalent to about 1 lb. per unit increase or decrease in litter size. It will be noted that deviations from regression are remarkably small for gilts' litters. Whether there is a biological basis for this is doubtful.

The fact that a straight regression line can be fitted to this type of data should not blind the investigator to the possibility that the relation between weaning weight and size of litter is not really linear. On the

contrary, there are *a priori* reasons for thinking that the regression line which has been fitted is misleading. The factors which are known to affect the growth of pigs up to weaning are hardly likely to interact in a simple way. The increase in milk production by the sow with increase in size of litter is not linear, nor is it probable that the change in efficiency of the pigs with varying quantities of milk is linear, so that considering these two factors alone, it is unlikely that the observed regressions are more than approximations. It may be shown, in fact, that a parabolic curve or a cubic curve may fit equally well the same data. Approximate equations involving square and cubic terms have been worked out for the data relating to the first litters, but the third and fourth terms of the equations are so small as to make it not worth while to carry this type of analysis any further with the present figures. The parabolic curve appeared to give a slightly better fit than the straight line and to be practically the same as the cubic curve. There would certainly be no significant differences among them.

Relation between growth of pigs and milk supply

As a descriptive statistic the linear regression coefficient probably fits as closely as any the net result of all the factors affecting weaning weight in relation to litter size. Nevertheless, the form of the curve plotted from the average weaning weights obtained from second to ninth litters suggests an explanation of results which do not conform to the straight regression line. The changes in average weaning weight shown in Fig. 1 indicate, if they are accepted for the moment at their face value, that there is a range of litter sizes in which there are no differences in average weaning weight, and which extends on either side to extremes of litter size where the average weaning weight is greater or less than in the central part of the range. Now although the numbers of litters on which this figure is based are too small to be of much significance *per se*, the fact that they agree in part with both of the opposed views as to the effect of litter size on weaning weight suggests an explanation by which these views may be reconciled.

Starting from the observation of Bonsma & Oosthuizen (1935) and Dschaparidse (1936) that the amount of milk per piglet falls off with increasing litter size although the total milk production of the sows rises, and assuming with the former that there are changes in the efficiency with which a piglet can deal with varying quantities of milk, the average weaning weight may be visualized as a function of these two variables.

It may be supposed that the amount of milk that a pig receives will vary according to the size of litter, on the grounds that increasing stimulus by suckling will not result in equal but in diminishing increments of milk, and that, when the number in a litter exceeds the number of teats, the available milk must be shared. It may also be supposed that after the maintenance requirements are satisfied the growth of a pig will be in direct proportion to the amount it receives until the quantity reaches a certain point, after which the gain in weight per unit of milk consumed over maintenance requirements will gradually fall as the quantity of milk increases. Assuming that weight at weaning is a function of these two variables, the change in average weight with change in litter size shown

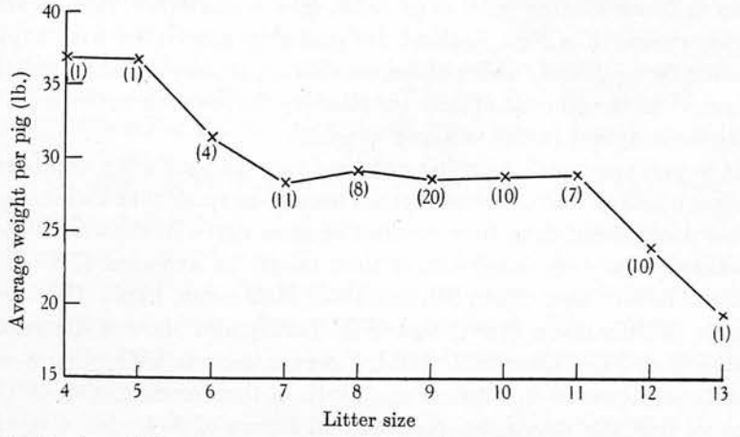

Fig. 1. Showing relation between mean weight per pig at weaning for litters of differen sizes excluding gilts' litters. (Number of litters in brackets.)

in Fig. 1 may be interpreted in the following way. Over the range of 7–11 in litter size, increased economy of gain has offset any reduction in milk supply. In litters larger than 12 this did not happen, and the average weight decreased. In litters smaller than 7 the reduction in economy of gain is more than offset by the rapidly increasing quantity of milk and the average weight rises. Hypothetical as this suggestion may be, it offers an explanation of the diverse results obtained from different experimental herds. Johansson (1931) for instance, found that at 3 weeks there was very little change in average weight per pig for litters of 10–19 pigs. Below 10, the average weight increased fairly rapidly. Such results might be expected if high fertility and heavy milk production went together, or if there was special feeding of sows with large litters, for in both these circumstances the amount of milk and the average weight per pig (but

presumably not the economy of gain) would be relatively high in the large litters.

In the New Zealand results previously mentioned there was no definite change in average weaning weight with litter size. The explanation for this would appear to be that various breeds were used in the compilation of the results; those breeds characterized by low milk production and low fertility would depress the weaning weight of the pigs in small litters, while those of high fertility and milk production would raise the weaning weight of the pigs in large litters. The same thing could happen within a breed consisting of strains differing in fertility and milk production. Another factor which would probably tend to level out differences between litters is creep feeding with skim milk. The remarkably high weaning weights recorded in New Zealand are probably associated with supplementary feeding, and, under these conditions, it may be expected that differences in the amount of milk supplied by the sow will not be reflected to the same extent in the weaning weights.

It is perhaps worth pointing out here that although the numbers of litters containing four or fewer pigs are usually so small that little reliance is placed on them, data from various sources agree in showing a lower growth rate for very small litters than might be expected (*Bull. N.Z. Dep. sci. industr. Res.*, 1930; Blissett, 1932; McMeekan, 1936). The 3-week weights of Johansson (1931) and Wild (1927) also show a decrease in passing from 3 in a litter to 2. Wild, however, records his highest 8-week weights for litters of 2. Lush *et al.* (1934), in their examination of birth weights, find the maximum occurring in litters of 3–4 with a distinct decrease with litters of 2. As Lush remarks, the conditions responsible for very small litters seem to be inimical to the development of very heavy pigs, but whether the conditions effective during gestation are also effective up to weaning has yet to be discovered.

Fertility and milk production

Hammond (1926) has pointed out that sows which are very fertile have usually a good milk supply. This may mean simply that as litter size increases, the number of teats used and the total quantity of milk produced rise. In so far as increased economy of feeding by the young pigs or early supplementary feeding counteracts the effects of a reduced amount of milk per pig, weaning weight will not be affected by increased litter size, and the more fertile sows will have the appearance of being particularly heavy milkers. On the other hand, it is conceivable that the milk yield of very fertile sows is higher than it should be on this argument. The frequency with which large litters approach much smaller ones in weaning weight per pig suggests that there is possibly relatively more milk available for the large litters than would be expected if the increase were due entirely to more teats being used. Both fertility and milk yield are closely connected with the functioning of the pituitary gland, and it may well be that large litters and heavy milking go together because of the possession of an active pituitary. As a rough test of this possibility, the records were examined and two groups of sows selected from them, namely, those which raised 8–9 pigs, after farrowing at least 5 more than this number, and those which raised 8–9 pigs after farrowing not more than 11. Excluding gilts' litters, there were only 11 and 7 litters respectively fitting this description. The former, which should have had the heavier weaners, actually had the lighter. More instructive results could be obtained by raising large and small litters on sows of known high fertility and sows of known low fertility and recording birth weights and 3-week weights.

Variation in weaning weight in litters of the same size

The interpretation of the meaning of variations in weaning weight has much practical importance. As between herds, of course, all differences could be attributed to feeding, climate and related factors, and particularly to the herdsmen. But within the herd it is of importance to know why there is such a large variation in the average weaning weight for litters of the same size.

From the figures in Table II it can be quickly calculated that the percentage of the total variance made up of differences between average weights of litters of the same size is approximately 78, 71, 68 and 41 per cent for first, second, third and fourth–ninth litters respectively. There appears to be a reduction in variance with increasing age of the sow, but this may well be due to the effect of eliminating the poorer sows. If this were so, the explanation that this portion of the variance could be largely attributed to differences in milk supply (as distinct from differences in milking capacity) of the sow would receive some support. Comparison of the variance (mean square) within classes with the total variance shows that with the exception of the last pair the differences are negligible. That is to say, the variation in average weight is just as great for any one size of litter as it is for all litters together, regardless of size. It would seem, therefore, that in the Edinburgh herd litter size is a relatively unimportant, although real, source of variation, except perhaps where old tried sows are concerned.

Litter sampling

Although the essence of the litter-testing schemes for the improvement of performance in pigs is the raising of samples of litters under standard conditions, there appears to be very little information as to the relation between such samples and the litters from which they came. As a rule the choice of sampling method depends on the nature of the variation in the population to be sampled and on the degree of accuracy which it is desired to attain. The generally adopted plan of using four pigs from a litter seems to have arisen from the conflict of economic and biological considerations. It may well have been assumed that the larger the sample the better the estimate of the whole, but obviously the costs of maintaining establishments for raising larger samples would be excessive and the scope of the schemes would be reduced. In these circumstances the feasibility of litter testing may be regarded as dependent on the fact that a fair measure of the litter may actually be obtained from a sample no larger than four. Useful results might still be obtained of course, even if the sample itself were not of much significance, by the incidental focusing of attention on performance and husbandry.

Variation in pigs is well known to be associated with differences in breed or strain, breeding and feeding methods, climate and so on, so that the optimum sampling method will probably not be the same under all circumstances. Nor is it difficult to envisage a situation in which economic factors may make a sample of four too large, and then the question arises as to whether a smaller sample is worth while. In addition to the size of the sample, the way in which it is taken is open to variation. From a litter of 10 pigs for instance, it is possible to obtain 210 different combinations of four pigs. In practice a request is usually made that a "representative" sample of four "average" pigs should be sent to the Testing Station.

The Scandinavian Testing Stations ask for 4 pigs, 2 male and 2 female, which are close to the average weight for the whole litter. Reports from the Danish Experimental Laboratories (Beck, 1933) show that it is not always practicable to send in the ideal sample. The sexes are often not evenly distributed, and the variation in weight of the individual pigs may be rather large so that one or two animals in the sample depart widely from the average. The Danes apparently do not place so much importance on the actual similarity of the average weights of litter and sample, for they ask that the sample pigs shall be even and large for their age. This is

largely due to the fact that they observed that mortality was higher among the lighter pigs than it was among the heavier. Also the tests were not deemed to have begun until the pigs had reached 20 kg. in weight.

The Swedish Testing Stations (Bengtsson, 1934) required the sample to have the same average weight as the litter, and considered that if the discrepancy between them was not more than 1 kg. the accuracy of the test would not suffer. It was suggested that for the purposes of calculating the average of the litter, the commonly occurring runts or exceptionally small pigs should be neglected. The tendency for breeders to select pigs heavier than the average was considered a mistake, since the results of the test, although sometimes improved thereby, would give a less reliable estimate of the litter and of the breeding value of the parents. It was also rightly pointed out that the heaviest weaners did not necessarily give the best performance under test, for the factors governing their growth up to weaning were not the same as those governing it subsequently.

In a theoretical discussion of the accuracy of litter testing Lush (1936) states that the correlation between the average of a sample of n pigs chosen at random, and the average of the litter with t pigs, approaches $\sqrt{\frac{nr}{1+(n-1)r}}$ when t becomes very large, r being the correlation coefficient for litter mates for the characteristic measured. Having obtained values of r it is possible to calculate from this formula the effects of increasing the number in a sample on the accuracy of the test as a measure of the whole litter. According to this process there is a rapid increase in accuracy as the sample increases from 1 to 3 with further, although smaller, increases up to 5. Beyond this the increases are small, and constantly become smaller as n increases. All this applies to random samples. According to Lush, "If the test pigs are *selected* with intent to get a *representative* sample, the correlations should be higher where n is small, but would not rise at so rapid a rate with n. If the samples from some herds are intentionally selected to do better than is really typical of the litter, but are not so selected in other herds, the correlations should be lower than those pictured but would rise more rapidly with increasing n...." In what follows, it will be seen that actual sampling experiments give results which are in accord with these forecasts.

Since records have been kept of the growth of all pigs in the herd under discussion, and since the system of feeding has been kept constant, it is possible to calculate an approximate rate of growth for each pig by dividing the weight at completion of growth to bacon weight by the

number of days from birth required to reach this weight. From these individual records means have been calculated for various types of samples and for the litters from which they have been drawn.

The types of sample used are as follows:

(*a*) four pigs nearest the average of the litter;
(*b*) three pigs nearest the average of the litter;
(*c*) two pigs nearest the average of the litter;
(*d*) four heaviest pigs;
(*e*) four pigs chosen at random.

The first four samples were easily obtained. The random sample was secured by withdrawing numbered marbles from a hat in groups of four; the observed occurrences of the various numbers in test drawings were sufficiently close to the equality expected. All sampling was done without respect to sex. Lush (1936) has shown that as far as rate of gain is concerned, sex differences are negligible. After selection of the samples the mean rate of live-weight increase was found for each and compared with the mean for the whole litter, including the sample. This process gave the results presented in Table III.

Table III. *Mean daily rates of live weight increase obtained by various methods of litter sampling (at weaning)*

Litter size	No. of litters	Rate of daily live-weight increase in lb. Whole litter	Median four	Median three	Median two	Heaviest four	Random four
12	8	0·878	0·900	0·898	0·910	0·927	0·869
11	8	0·957	0·963	0·951	0·969	1·003	0·923
10	11	0·994	0·998	1·003	0·989	1·027	1·011
9	24	0·978	0·981	0·982	0·972	1·011	0·953
8	19	0·980	0·983	0·992	1·002	1·012	0·983
Loss of information %			8	16	34	15	10
Correlation between average rates of live-weight increase for samples and whole litters		$r=0·96$	0·92	0·82	0·93	0·95	

To facilitate comparison of the results Table IV has been compiled from the previous one by subtracting the mean rate of live-weight increase per day of the sample from that of the litter and multiplying the difference by 200 which gives an estimate of the average difference in weight at the end of 200 days between a pig of the sample and a pig of the whole litter. It then appears that the choice of the heaviest pigs for the test would give a better result (from the point of view of getting high performance from test pigs) than any other type of choice. This is to be expected in view of the positive correlation between the weight of a pig at weaning and its weight about 150 days later. The fact that the deviations are all positive and comparatively large shows that such a sample does not give an accurate estimate of the litter as a whole. The actual difference, 6–11 lb., is, however, small. The remaining types of samples do not appear to yield any noteworthy differences.

Table IV. *Table showing mean differences between sample and whole litter multiplied by* 200 *to give an estimate of the average difference in weight at* 200 *days between pigs of the sample and of the whole litter. Differences calculated from the preceding table*

Litter size	No. of litters	Estimated mean difference in lb. from whole litter: Four pigs nearest average	Three pigs nearest average	Two pigs nearest average	Heaviest four pigs	Random four pigs
12	8	+4·4	+4·0	+6·4	+ 9·8	−1·8
11	8	+1·2	−1·2	+2·4	+11·2	−6·8
10	11	+0·8	+1·8	−1·0	+ 6·6	+3·4
9	24	+0·6	+0·8	−1·2	+ 6·6	−5·0
8	19	+0·6	+2·4	+4·4	+ 6·4	+0·6

The fact that all the differences were positive for the sample of 4 pigs nearest the average is probably without significance. Considering now the results from the standpoint of the litter classes, there does not appear to be any consistent change in any of the samples, with the possible exception of the largest litters (12 pigs), the samples from which gave positive and comparatively large differences from the litter averages (excluding the random sample). The performance of the random samples from litters of 11 and 12 pigs suggests that the occasional inclusion of the smallest pigs has been responsible for the distinction which has arisen between these samples and the remainder which do not include the smallest pigs. In litters smaller than 11 the occurrence of exceptionally small pigs is not so frequent, and therefore does not affect the random sample to the same extent.

In order to obtain a more comprehensive expression for the relation between performance of litter and sample, the coefficient of correlation between them was calculated from the average live-weight increase of each per day. The values of r given in Table III represent the degree of correlation irrespective of litter size. Before the data were combined an analysis of variance was made to determine whether there were significant inter-litter class differences in the behaviour of the sample. This was done by calculating the variance of the observed deviations of sample from litter average about the mean deviation. With the exception of the random sample, all cases gave no significant inter-litter class difference and the results were accordingly combined in the estimation of the coeffi-

cient r. For the random sample, the value of z corresponding to inter-litter class variance lay between the values for the 1 and 5 per cent points as given by Fisher (1936). This result arose from consistent negative deviations in litter classes 11 and 9, for which no explanation can be offered. The estimates of r were then made from each litter class separately, but since they were as similar as could be expected with random sampling in such circumstances, the values have been combined by means of the z transformation. From these values of r, "loss of information" has been calculated as equivalent to $1-r^2$, and expressed as a percentage.

It is interesting to compare these results with the answer to the question of what was gained by testing four litter mates instead of any other number provided by Lush (1936) from intra-litter correlations. Using his expression for the value of the coefficient of correlation (r) between average of litter and sample, $\sqrt{\left(\frac{n}{t}\cdot\frac{1+(t-1)\,r_{00}}{1+(n-1)\,r_{00}}\right)}$, and substituting values 2, 3, 4, for n, the number in the sample, and the value 0·3 for the coefficient of correlation (r_{00}, see later) among litter mates, we obtain ~~0·57, 0·69, 0·78~~ for the values of r for samples of 2, 3, 4 respectively, drawn from litters of 10 ($t=10$). The observed values ($t=8-12$) are ~~much~~ higher, namely, 0·82, 0·92, 0·96. These observed values are, however, derived from "representative" and not random samples, as stipulated by Lush. In this case, he expected that the correlations would "be higher where n is small, but would not rise at so rapid a rate with n". This is partly borne out by his data, although the degree of correlation is rather higher than would be expected. The effect is to make samples of 4 sufficient for a very good estimate of the litter. To increase the sample to 5 would, on Lush's figures, give an appreciable improvement in the estimate, but in the present instance the improvement would certainly not be worth the trouble and expense. The high values of the coefficient require an explanation. The random sample which was taken yielded a composite value of 0·95 from components varying between 0·89 and 0·98, as compared with 0·78 expected from Lush's formula. The discrepancy apparently arises from the use of a coefficient of correlation between litter mates which is too small. If the coefficient were to rise to 0·5 then the corresponding calculated value of the coefficient of correlation between sample and litter would increase to almost 0·9 with a sample of 4. The intra-litter correlation coefficient has been worked out for the two largest litter classes and found to be 0·5 for litters of 8 and 0·3 for litters of 9. These facts, together with the size of the correlation between samples and litters, must indicate that within litters the pigs were of a high degree of

similarity. At this point opportunity might be taken to point out that to use 4 pigs for a sample will not give equally accurate results (*a*) for all herds, (*b*) for all litters, or (*c*) for all qualities of the pigs, since the intra-litter correlation will vary continually. If, as is sometimes supposed, there is an increase in variability as litter size increases, then a sample of 4 pigs should give a more accurate estimate for small litters than for large ones. There is some slight evidence of such an effect in the present data (Table IV).

Relation between weaning weight and subsequent rate of gain

The foregoing comparison of samples and litters shows only that they behave in a very similar way, and does not concern itself primarily with the performances of the individual pigs. The intra-class correlation found for pigs within a litter has been seen to be for one litter class 0·3, and for another 0·5, indicating that within a litter there is a fairly strong tendency for the pigs to behave similarly. A somewhat different method of approaching the question is by estimating the regression of rate of live-weight increase on weaning weight. If there were a high degree of correlation between weights of pigs at weaning and at 200 days, the pig of average weight at weaning would still be the pig of average weight at 200 days of age. Litter testing would then require only one or two pigs from each litter. In practice, however, more are required. As the period of growth proceeds, therefore, there must be many changes in the order by weight into which the pigs sort themselves at weaning. As a measure of this, the regression on weight at weaning of rate of growth from weaning to 200 days was estimated for a portion of the population. Complete litters were used which were restricted in size to 8–10 pigs to avoid complications due to crowding and competition, and which gave a total of 203 animals treated in the calculations without further reference to litter. The regression of rate of live-weight increase on weaning weight was equivalent to 0·07 lb. per day for a difference of 1 lb. in weaning weight.

Table V. *Analysis of variance in rate of growth of sample of 203 pigs classified according to weaning weight*

Variance	D.F.	Sum of squares	Mean square	S.D.	$\log_e$	z
Linear regression	1	45·64	45·64	6·756	1·9104	1·6777
Deviations from regression	8	24·98	3·12	1·767	0·5693	0·3366
Within classes of same weaning weight	193	307·38	1·59	1·262	0·2327	—
Total	202	378·00	1·87	—	—	—

An analysis of the variance is given in Table V, which shows that the variance of pigs of the same weaning weight was 1·59 (S.D. = 1·26).

The probability that a value of z as large as 1·67 would occur by chance is much less than 0·1 per cent. A linear regression, however, appears insufficient to express all the facts, for, on estimating the non-linear regression variance, a value is obtained which is large enough to reach the 5 per cent point of significance.

The intra-class correlation obtained from $\frac{1{\cdot}87-1{\cdot}59}{1{\cdot}87}$ is 0·15. This is one way of expressing the fact that there was a considerable range of variation in the subsequent rate of growth of pigs of the same weaning weight. In other words, many pigs which are heavy at weaning do not maintain their relative superiority, and herein lies the difficulty of selecting pigs for breeding at early stages. Several factors affecting weaning weight are dealt with in the first part of this paper, and there are without doubt many others. Consequently, it is not easy to decide why a pig is small at weaning, but the factor or factors responsible must be supposed to have some bearing on its future performance. Causes of poor pre-weaning growth that may have lasting effects, preventing an animal from doing well under any circumstances, may be genetically inferior stamina or permanent injury following starvation or disease. Other causes may not be accompanied by inability to respond to improved environment. Included here would be various nutritional deficiencies of quality or quantity. Pigs affected by the latter may well show enhanced growth after weaning. That such cases are common is apparent when weight records taken at frequent intervals are available. These often show that for some reason or other an animal receives a check to growth and then recovers. Frequent occurrence of this phenomenon would explain much of the high intra-class variance shown in Table V.

Analysis of variance in growth rate from birth to 200 days

An analysis of variance has also been made of the growth of pigs belonging to litters of 8 and 9, the growth rate in this case being calculated from the weight at completion (about 200 lb.) and number of days (about 200). In this way an estimate of the variance between litters and of the correlation between litter mates has been obtained.

For both litter classes the values of z are significant, the probability of such values being reached by chance being much less than 1 in 1000. There is, therefore, a part of the variance which is not accounted for by

random sampling of litters with a variance of their own. This may be expressed in another way by saying that there is a significant correlation between litter mates.

Table VI. *Analysis of variance in rate of growth from birth to bacon weight*

Variance	D.F.	Sum of squares	Mean square	S.D.	log S.D.	z
		Litters of 8 pigs				
Between litters	18	1·5546	0·0864	0·2939	2·7753	1·1292
Within litters	133	1·2008	0·0090	0·0950	3·6461	—
Total	151	2·7554	0·0183	0·1351	—	—
		Litters of 9 pigs				
Between litters	23	1·3088	0·0569	0·239	2·5686	0·7759
Within litters	192	2·3148	0·0121	0·110	3·7929	—
Total	215	3·6236	0·0168	0·130	—	—

The information may be summarized as follows:

	Litters of 8	Litters of 9
(1) Mean daily gain	0·987 lb.	0·986 lb.
(2) Standard deviation:		
(*a*) All pigs	0·135	0·130
(*b*) Pigs in a litter	0·095	0·110
(3) % of total variance due to differences between litters	56 %	36 %
(4) Correlation between litter mates	0·52	0·29

It will be noticed that except for the differences between litters and the correlation which depends on it, there is considerable similarity in the performance of the pigs of the two classes. The differences between litters amounting to 56 and 36 per cent are not significantly different from each other. The total variance found here for the growth rate from birth to 200 days is practically the same as that for the sample of 200 pigs mentioned in the previous section, whose growth rate was calculated from weaning to 200 days.

Discussion

It is pertinent to ask whether the intra-litter correlations discussed have any significance from the point of view of breeding, and, if so, to what extent they are an indication of the possibilities of improvement by selection. The existence of an intra-class correlation here indicates that the portion of the total variance existing between litters is not wholly accounted for by random sampling. There are, therefore, differences between litters, and a degree of similarity of litter mates which must be

attributed to certain factors which affect them, but not other pigs. Such factors are genetic and environmental, the latter including the various aspects of the mothering ability of the sow. With the present data it is not possible to arrive at an estimate of the relative importance of these two types of factors, but there is a certain amount of evidence from other sources. Assuming that rate of growth is governed by many genes with additive effects, and that the effects of dominance, epistasis, and correlation between parents' genotypes are negligible, the correlation between litter mates, r_{00}, is equal to $e^2+h^2/2$, where e represents environmental and h hereditary effects (Lush, 1931). If e^2 were zero, h^2 would reach a maximum of 0·6 when r_{00} was 0·3, as it was found to be for a particular case. This 0·6 would then represent the portion of the individual variance which was due to additive gene effects. This value is almost certainly too large because environmental effects on such a character as rate of gain are very probable and would influence it more than such a character as body length. From his investigations of the results of Danish Litter Testing Stations, Lush (1936) comes to the conclusion that about 25 per cent of the total variance may be attributed to genetic causes. Since the litter-mate correlation was estimated at 0·24, the portion of the variance due to e^2 becomes 0·12, that is about 12 per cent. With somewhat larger values for r_{00}, such as those obtained, either h^2 or e^2, or both, may be greater, but in any case there would seem to be room for improvement by selection. It might be expected that, applied to rate of gain, selection could operate in two ways, first, by changing the mean growth rate as a result of breeding from genetically superior animals, and secondly, by increasing milk yields of sows; for if rate of gain is calculated from birth to age at bacon weight, e^2 will include variance due to differences in milking capacity of sows which itself is probably subject to additive gene effects.

The intra-litter correlations found by Lush (1936) and Berge (1936) are lower than those observed in the Edinburgh material. Owing to the comparatively small material, the sampling errors attached to the latter are rather high, so that the values of 0·3 and 0·5 obtained are not significantly different. Even the lower of these is larger than the values of 0·24 and 0·19 obtained by Lush and Berge respectively. Some of the differences may be accounted for by the fact that the rate of growth in the Edinburgh material was calculated from birth, whereas the Danish and Norwegian growth rates were calculated from beginning of test after weaning. The correlation derived from them does not, therefore, include differences of environment between litters up to weaning.

On the assumption that the Edinburgh herd is typical of the pigs of

Great Britain, it must be concluded that the success which has followed litter testing in Scandinavian countries would be repeated here. Differences in growth rate (which are probably partly genetic in origin) exist, and it may be assured that except for minor differences they can be detected with considerable accuracy by samples of 4 pigs per litter tested.

Summary

1. Following an examination of weaning weight with respect to litter size, it is concluded that no general relation between the two exists. Although a significant regression of weight on litter size was found, it appears probable that in herds where the relation between fertility and milk yield is different, such a regression will not necessarily be found.

2. A sampling experiment was carried out to determine the extent to which a sample might be expected to represent the whole litter. A correlation of 0·96 was found between the mean growth rate of samples consisting of the four pigs nearest the average at weaning and the mean of the whole litter. This represents a loss of 8 per cent of the information. With three or two pigs chosen in the same way the loss was greater. Samples of four pigs chosen at random did not give results significantly different from those of the four pigs nearest the average. The choice of the heaviest four pigs resulted in a loss of 15 per cent of the information.

3. The slight difference between the results from the random sample and the sample of the four average pigs indicated that there must have been only a small correlation between weaning weight and subsequent rate of growth. An analysis of post-weaning rate of growth showed that the intra-class correlation of pigs of the same weaning weight was 0·15. Individual weight at weaning would therefore appear to be of slight value in estimating subsequent performance of pigs of same weaning weight.

4. Intra-litter correlations of growth rate for litter classes eight and nine were found to be 0·3 and 0·5. These values are higher than those found by others, probably as a result of the inclusion of the pre-weaning period in the calculation of the growth rates. There would appear to be grounds for believing that at least a fifth of the individual variance may be accounted for by additive gene effects.

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A. D. BUCHANAN SMITH AND H. P. DONALD

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By A. D. BUCHANAN SMITH and H. P. DONALD

Institute of Animal Genetics, University of Edinburgh

(With Three Graphs)

CONTENTS

Introduction

A considerable volume of recent work has made it clear that carcass quality is closely bound up with breed, strain and type of pig, and with rate of growth. In addition to the reports of the Scandinavian and German Pig Testing Stations, the investigations of Schmidt *et al.* (1934), French & Emson (1936), Lush (1936), Shaw & McEwan (1936), Kliesch (1937), McMeekan (1937), Hammond & Murray (1937) and others, agree in emphasizing the importance of genetic constitution. Rate of growth studies may obviously take a variety of forms. That which deals with the differential rates of development of muscle, fat, and bone has been greatly advanced by the long series of researches by Hammond (1932*a*, *b*), in which he has made it clear that even genetically similar animals cannot be expected to have the same carcass measurements unless they have been exposed to the same environmental conditions throughout

their growing period. Another form has been concerned directly with the effects of diet on carcass quality, the results of which have been reviewed by Callow (1935). Some types of diet can result in too much or too soft fat, and deficiencies of particular constituents appear to be more detrimental to quality than excesses. Woodman *et al.* (1936), for instance, could find little or no effect of their high protein rations on carcass quality, nor could McMeekan (1937) with a very different type of diet. A much less extensive examination of the influence of rate of growth on carcass quality has been made on standard rations, but the work of Petersen (1936) and Mansfield *et al.* (1937) shows that this factor must be taken into account.

The problem of growth rate in relation to age and weight may be resolved into determining the response of animals to variations in type of environment, or into determining the variations in response within a given environment. The latter alternative has been followed by Berge (1936) and Vecchi (1934), who observed the growth of pigs during restricted periods and noted that the faster growing of two breeds in the early stages became the slower growing during the later stages of the test period. That litters within a breed can be distinguished effectively by their growth rates over a range smaller than 40–200 lb. will be shown in this paper. If these differences are ultimately traced to genetic causes, an extension of the idea of breed precocity to strains within a breed will be possible. With the knowledge that fast growth is more desirable at some stages of development than at others, a more satisfactory avenue for selection would be opened up, together with a promising application of the growth and form theory linking growth rates and carcass quality.

In the present work existing variation in the growth of bacon pigs has been studied in some of its aspects, with the object of deciding whether further analysis on these lines is likely to prove profitable. This is necessarily the first step. The next is to determine whether the observed litter differences are heritable and whether they are accompanied by corresponding carcass differences. This report becomes, therefore, a consideration of the variation in growth during certain defined periods, with special emphasis laid on the relation between the gains made during successive periods. With this definition of its scope, the opportunity has been taken of including some reference to the significance of weaning weight. The emphasis placed on the importance of heavy weaners has led to some misapprehension as to the meaning of the underlying correlations between weaning weight and subsequent growth. As a practical step towards more economical production, the raising of average

weaning weights has a clearly established value, but insistence on the correlation of weaning weight with subsequent growth has the disadvantage that it focuses attention on the weaner rather than on the important factor in rearing heavy weaners—the milk production of the sows.

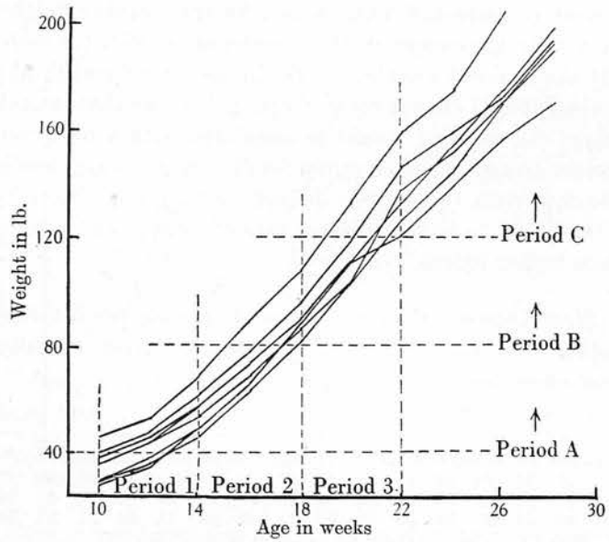
Material and methods

The material for this investigation has been provided by the observations made since 1931 on the Large White herd of pigs maintained by the Institute of Animal Genetics at Edinburgh. The type of management and the rations for all classes of stock have been unchanged throughout with the exception of an alteration in the feeding of dry sows at the end of the first year. Litters were weaned at 8 weeks and thereafter weighed fortnightly, and fed quantities of a standard ration determined by the amounts eaten promptly on the first day of each fortnight. Litters were raised complete—a method which enabled the food consumption to be calculated, but may have been disadvantageous to light weight members of a litter.

The principal part of this work has been the study of the variance and covariance of the increases in weight put on by the pigs during three periods of 28 days. In section A of this paper, these were 10–14, 14–18 and 18–22 weeks. The growth of each litter was graphed to permit easy interpolation where the weighing days did not coincide with the ends of the periods, and to indicate clearly erroneous weighings. A pig's weight is, of course, constantly changing, and any practicable method of dealing with large numbers of animals can only give an approximation to the actual gains in weight. Periods of 28 days were chosen partly in order that the errors of weighing should not be large in proportion to the weight increase, and partly to ensure at least three subdivisions of the growth curve.

In section B of this paper, a different method of fixing the 28-day periods has been used, in order to determine what alteration takes place in the variability when increases from the same weight are considered instead of the increases from the same age. Graph 1 shows a litter record subdivided vertically into three periods in which the pigs are all the same age, and horizontally into three periods in which the pigs all begin at the same weight. To distinguish the two type of periods, those beginning at a constant age are called periods 1, 2 and 3, while those beginning at a constant weight are called periods A, B and C. A slight modification of periods A, B and C was also used, which will be described later.

The gains shown by the individuals of a litter in any period were summed and averaged to give the "mean increase". From the sums of squares of the individual gains, the variance of the gains, $Sx^2/(n-1)$, was obtained for each litter, and is referred to as the "mean square". No distinction has been paid to sex, since Berge (1936) and Woodman *et al.* (1936) found only a slight difference over the whole test period, and the conditions of the present investigation did not warrant the



Graph 1. Growth curves for a litter of six pigs from 10 weeks of age, showing the method of subdivision into periods defined by age and weight.

refinement of separating the sexes. It is possible, therefore, that neglect of sex differences may have obscured the results to a slight extent.

For the study of the variability of the increases, the method adopted has been to analyse the variance of the mean square together with its covariance with the corresponding mean increase per litter. To assume that the variability would be proportional to the increases was considered inadvisable, and the method of analysis of Day & Fisher (1937) which avoids this assumption was applied.

A. *Periods defined by age*

The mean increase in weight per pig and its variation.

The mean increases in weight per pig per litter and their associated mean squares have been classified into groups according to period, litter

size and average weight of litter at weaning. The averages for these groups are contained in Tables I and II. Although there is a tendency for the mean square to be greater when the increase per period is greater, the relation between the two as determined by litter size groups is far from being regular. While the increase per pig remains fairly constant in each period from one litter size to another, the mean square varies considerably but not regularly with change in litter size. The relation between mean increase and mean square for the weaning weight groups seems clear. With the exception of the mean squares for the rather small group with the heaviest weaning weight in the second and third periods, the values in Table II change regularly in such a way that in each period a lowering of the weaning weight is associated with a reduction of the mean increase and with higher values for the mean square (see Graph 2). That is to say, with the periods defined as they are, litters heavy at weaning time tend to have a greater rate of growth and a lower mean square than lighter litters.

Table I. *Mean increase in weight in pounds per pig per litter and corresponding mean square classified according to period and litter size to nearest whole number*

Litter size ...	6		7		8		9		10		11		12		Average	
	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.
Period 1	23	35	24	22	21	36	22	36	21	26	22	31	20	32	22·0	31·0
Period 2	31	31	29	38	30	33	29	49	30	36	29	40	28	43	29·2	39·3
Period 3	35	51	35	39	34	50	36	51	37	34	32	49	34	37	35·1	46·0
No. of litters	10		26		27		32		19		13		8		135	

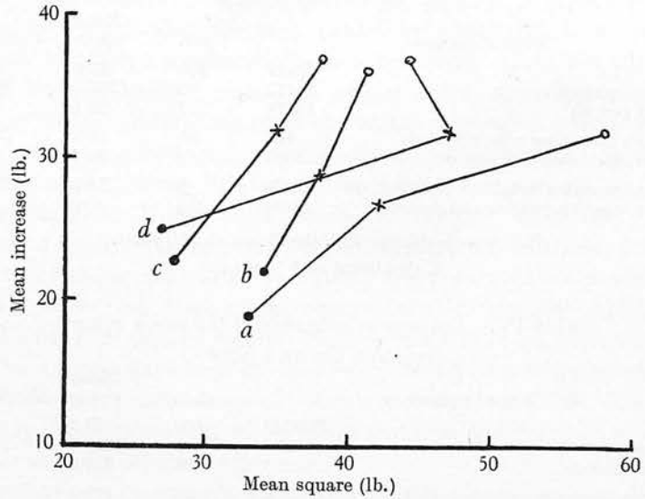
Table II. *Mean increase in weight in pounds per pig per litter and corresponding mean square classified according to period and weaning weight to nearest whole number*

Weaning weight ...	22±2		26±2		30±2		34±2	
Period	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.
1	19	33	22	34	23	28	25	27
2	27	42	29	38	32	35	32	47
3	32	58	36	41	37	38	37	44
No. of litters	40		40		37		18	

Since the amount of variation within and between litters is so large it is unsafe to draw any definite conclusions from the averages given above. Statistical analyses have therefore been made in order to estimate the importance of those sources of variation which most

probably have had a real effect on the increases and their mean squares. Table III shows the relative importance of periods, litter sizes and weaning weights on the mean increase in weight per pig during 28 days.

From these figures it appears that the mean increase in weight per pig is substantially affected by its weaning weight as well as by the period in which the growth takes place. These results are entirely to be



Graph 2. Effect of weaning weight and period on the relation between mean increase in weight and its variability (mean square).

Period	Weaning weight
1 •—	*a* 22±2 lb.
2 —×—	*b* 26±2 lb.
3 —○	*c* 30±2 lb.
	d 34±2 lb.

expected. The normal growth curve of a pig shows (Berge, 1936) that the absolute rate of increase in weight becomes faster until bacon weight is approached. The heavier a pig is at weaning, therefore, the faster will it tend to grow in all periods. Litter size has had no effect on the increase.

A similar analysis for the mean square for each litter is given in Table IV.

Period and weaning weight class again had real effects, the mean square increasing from first to last period, and decreasing as weaning weight increased (Tables I and II). The influence of litter size was again

without significance. None of these three variables was really effective in controlling the observed variation. Even by removing the variance due to period, the mean square was reduced by less than 5%, whereas the same process applied to the variance in mean increase reduced the mean square by 44% (see Table III).

Table III. *Analysis of variance of the mean increase per pig during 28 days*

Sum of squares		D.F.	Mean square	Significance
Total	25847	400	64·6	
Between periods	11473	2	5736·5	S.S.
Within periods	14374	398	36·1	
Between litter sizes within periods	441	18	24·5	N.S.
Within litter sizes and periods	13933	380	36·7	
Between weaning weights within periods	1926	9	214·0	S.S.
Within weaning weights and periods	12448	389	32·0	

N.S. non-significant; S.S. significant at 1% point.
S. significant at 5% point.

Table IV. *Analysis of variance of the mean square deviation for each litter*

Sum of squares		D.F.	Mean square	Significance*
Total	308518	400	771·3	
Between periods	15265	2	7632·5	S.S.
Within periods	293253	398	736·8	
Between litter sizes within periods	14934	18	829·7	N.S.
Within litter sizes and periods	278319	380	732·4	
Between weaning weights within periods	12894	9	1432·7	S.
Within weaning weights and periods	280359	388	722·6	

* As in Table III.

The variability of individual increases in weight.

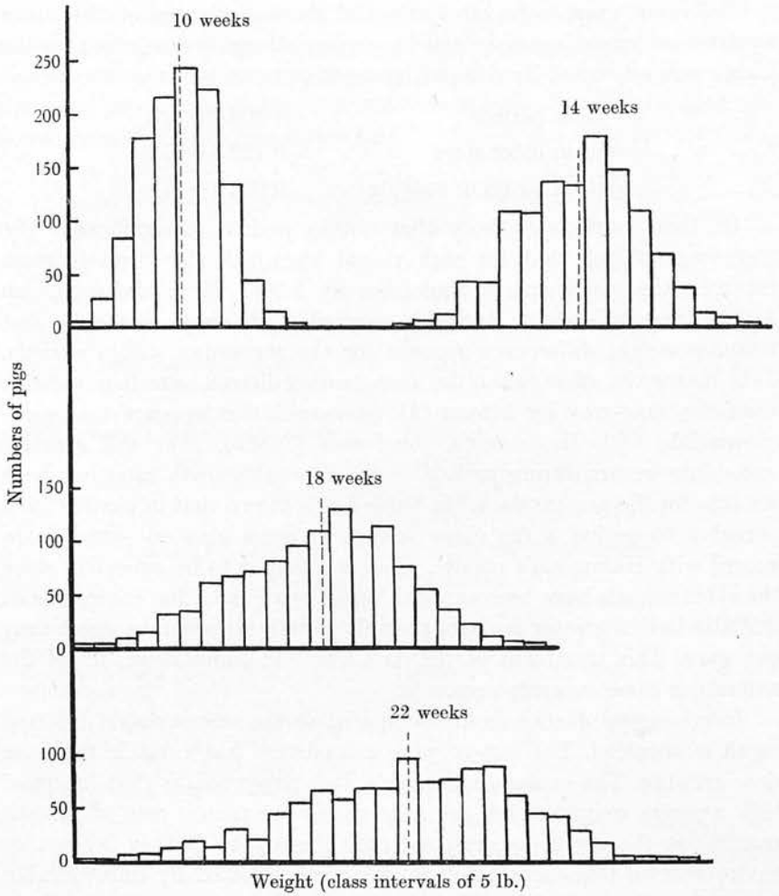
The factors which have been shown to influence the variability of the increases (in the preceding section) may do so through their effect on the increases themselves. Lacking evidence on the point, it might be assumed that as the increase in weight becomes larger, its variance is augmented in proportion. This assumption is made if the variabilities are compared by means of the coefficient of variability. In fifteen out of the twenty-one groups of Table I, however, the covariance of the mean increase with the mean square was negative, and the assumption becomes of very doubtful validity. On the contrary, it appeared as though there was a tendency within each subdivision of the data for the mean square to diminish as the mean increase became larger.

Following graphical examination of the covariances of the mean squares and mean increases, the linear regressions of the former on the latter were estimated by calculating coefficients, as follows:

Within periods	$-1{\cdot}206 \pm 0{\cdot}226$
Within litter sizes	$-0{\cdot}172 \pm 0{\cdot}172$
Within weaning weights	$-0{\cdot}042 \pm 0{\cdot}177$

Of these coefficients, only that within periods is significant. The regression is such that for each pound by which the mean increase enlarges, the mean square diminishes by 1·206. Since the regression within weaning weight classes is negligible, it seems probable that weaning weight differences account for the regression within periods. This means, in effect, that the fast-growing litters were less variable than the slow-growing litters. At first sight this appears to be incompatible with Hammond's conclusion (1932*b*), that the greatest variability occurs during periods of the greatest growth rate, but both are true for the present data. In Table I it is shown that in passing from period 1 to period 3 the mean square becomes greater—which is in accord with Hammond's results. Such a result is to be expected, since the older animals have been exposed longer to a fluctuating environment, and also have a greater range of possible growth rates within which they can vary. This treatment of the data involves comparisons of all the animals at three separate ages.

If subgroups of animals are compared at the *same* ages, a different result is obtained. The fast-growing animals are less variable than the slow growing. The explanation of this, it is suggested, is that litters of high average weight which are near to the maximum rate of growth possible at the given age, respond only slightly to further favourable environmental influences, and are not much affected by unfavourable influences, whereas litters of low average weight can respond greatly to stimuli in either direction. A consequence of this is that the distribution of ages at a given weight (Berge, 1936), or weight at a given age is markedly skew. It is relevant in this connexion to recall that Kapteyn (1903) discussed the occurrence of skew curves in biology and suggested that they might be made into normal curves by the use of a suitable transformation whenever the skewness was due to a regular change in the variable by which the organisms were measured. Whether such a regular change accounts for all the skewness apparent in the distributions shown in Graph 3 may be doubted. The distributions were obtained by classifying the weights of animals at the ages of 10, 14, 18 and 22 weeks,



Graph 3. Frequency diagrams showing distribution of pigs in weight classes at the ages of 10, 14, 18 and 22 weeks. The means are shown by dotted lines, the actual values being given in Table V.

Table V. *Table showing the characteristics of the frequency distributions of the weight of pigs at intervals during growth. With the exception of the means, the values given apply to the arbitrary units of 5 lb.*

Weeks old	10	14	18	22
Mean (lb.)	35·77	58·00	87·27	122·24
S.D.	1·76	2·75	3·79	5·01
$\sqrt{\beta_1}$	−0·0067	−0·0956	−0·2199	−0·2712
β_2	2·611	2·685	2·660	2·709
No. of pigs	1168	1143	1126	1098

and their descriptive statistics are given in Table V. The skewness, although not apparent at 10 weeks, becomes marked as the age increases. The observed skewnesses are 0·1, 1·3, 3·0 and 3·6 times their standard error (0·074 for $N = 1100$), so that the last two are significant. Similarly, the 5% value for the coefficient β_2 is about 2·76, so that all the observed values indicate a significant degree of flattening.

Whether a certain amount of skewness should be anticipated in the distribution of weights from a population of pigs need not be debated here. Most of the long negative tail actually observed can be traced to animals of subnormal growth at some time, animals which are growing at a rate commensurate with their weight rather than with their age (as will be shown later). These may be regarded as a separate population with characteristics different from those of the principal group. At any age their mean weight and growth rate are well below the average and consequently when combined with the principal group they contribute only to the negative side of the distribution. The increasing degree of skewness ($\sqrt{\beta_1}$) can be accounted for, since the increasing absolute rate of growth places the unchecked pigs relatively further and further ahead of the slower growing group.

From this brief examination of the changes in magnitude of variability under group feeding conditions, it may be reasonably deduced that the practice of allotting pigs to feeding groups according to weight is well founded. With this arrangement, the tendency for large discrepancies in weight to develop is checked at the outset, and a better control of individual growth rates is possible. Those who are interested in the growth rates and food consumptions of litters, however, cannot use this method. For them it seems likely that the advantages of decreasing variability, by reducing litters to a more or less even sample as small as four (Smith & Donald, 1937), will more than offset the loss of information involved by excluding members of the litters.

Relations between increases in weight in different periods.

The changes in variability noted above, although making the discovery of inter-litter differences more difficult, would not necessarily alter relative performances, as judged by the litter means. That they are, in fact, altered is shown by the correlations between the mean increases in different periods given in Table VI. Correlations between individual increases have not been calculated for the periods defined by age, and it cannot be assumed that they would be similar to those appropriate to the means. The coefficients of Table VI have been calculated for

various relationships of the four quantities—the means and their sum for the three periods, p_1, p_2, p_3 and P.

From these figures it will be noted that (1) litter size does not affect the coefficients; in fact, those for litter sizes 7, 8, and 9 are remarkably similar; (2) as befits their large contributions to the total, the increases in p_2 and p_3 are both strongly correlated with the total increase; (3) the influence of p_1 on P is smaller than that of p_2 and p_3 and is exerted mainly through its effect on p_2; (4) although $r\ p_2p_3$ is about +0·6, the partial correlations $p_2P.p_3$ and $p_3P.p_2$ are not greatly different from

Table VI. *Correlation coefficients for relation between average litter increases in different periods*

p_1, first period; p_2, second period; p_3, third period; $P=p_1+p_2+p_3$; n, number of litters

	Litter size					
	6	7	8	9	10	11
n	11	26	29	35	13	12
p_1P	+0·69	+0·63	+0·57	+0·62	+0·48	+0·27
p_2P	+0·84	+0·87	+0·83	+0·82	+0·93	+0·81
p_3P	+0·94	+0·90	+0·83	+0·81	+0·87	+0·80
p_1p_2	+0·44	+0·45	+0·37	+0·40	+0·45	+0·03
p_1p_3	+0·51	+0·37	+0·19	+0·18	+0·04	−0·14
p_2p_3	+0·69	+0·66	+0·50	+0·50	+0·72	+0·48
$p_1P.p_2$	+0·66	+0·56	+0·51	+0·55	+0·17	+0·43
$p_1P.p_3$	+0·73	+0·76	+0·74	+0·82	+0·90	+0·66
$p_2P.p_3$	+0·78	+0·85	+0·87	+0·83	+0·90	+0·82
$p_3P.p_2$	+0·92	+0·88	+0·87	+0·82	+0·79	+0·81
$p_2P.p_1$	+0·83	+0·82	+0·84	+0·79	+0·91	+0·84
$p_3P.p_1$	+0·94	+0·87	+0·89	+0·91	+0·97	+0·89

the total correlations p_2P, and p_3P; (5) eliminating the influence of p_1 has not greatly altered the correlation of p_2 and p_3 with P. There is thus a considerable degree of similarity in the performances of different periods. A correlation of +0·6 ($r\ p_2p_3$) is, however, far from being as large as desirable between two consecutive periods of 28 days, if the whole test period is to provide a reliable measure of breeding value. The circumstances giving rise to a coefficient of +0·6 must involve a considerable number of fluctuations in growth produced by influences either external or internal, or both. In so far as environment could be more strictly controlled at a testing station, these results constitute a justification of testing, for if the tested animals are themselves responsible for some of the relative differences in performance, the chances of detecting such differences would be greatly enhanced. Litters could, of course, not be judged solely by some standard such as growth rate per day from start of test. The best litters are then those with good performance in

all periods. This may appear to be all that is required, but, looking at the question from the point of view of carcass quality, another point arises. If it is proved that quality of carcass is associated with relatively slow growth in the latter stages, it would then become necessary to distinguish animals of this type from others having the same average over all performance, but showing comparatively slow initial growth followed by rapid fattening.

Under Edinburgh conditions, the performance of the litters in period 1, that is from 10–14 weeks of age, has shown a rather low correlation with subsequent performance, and must therefore have tended to obscure the inter-litter differences subsequently manifested. If it may be assumed, for practical purposes, that the immediate post-weaning history of a litter is without significance from the genetic standpoint, it would seem advisable to exclude from litter comparisons the data obtained from pigs which have not clearly adapted themselves to solid feeding. This is the procedure adopted for testing stations, and with good reason. It amounts to discounting that portion of the growth which may be directly or indirectly attributed to the uncontrolled nutrition whilst on the mother, since the length of the period to be disregarded will depend on the weaning weight. Evidence that it may be disregarded without affecting the subsequent results is offered in the ensuing section of this paper in which the pigs are compared on a weight instead of an age basis.

B. *Periods defined by weight*

Inter-litter differences.

The foregoing method of treatment of growth rate data gives results which depend on the actual performance of litters during specified periods which are the same for all pigs in all litters. It is a consequence of this that pigs which are small for any reason at the beginning of a period, are at a disadvantage throughout when absolute and not relative growth rates are considered. Litter averages and correlations which describe the performance of animals over long periods of their lives (e.g. average number of days from weaning to slaughter, correlation between weaning weight and growth rate from weaning to bacon weight) take no account of checks of various kinds, and no account of the relative but irrelevant disadvantage of the small pig, whose size may be merely a reflection of his dam's milking capacity. By the technique of calculation, it comes about that all environmental checks to growth are combined with any real genetical inferiority or superiority which may thus be effectually obscured.

These remarks may be illustrated by analyses made of the litters available in litter sizes 8 and 9. For these litters, the weaning weight has been compared with the actual increase in weight put on during three periods of 28 days each as before. In contrast to the previous calculations, the periods were chosen for each pig independently in such a way that the first (period A) began when the pig reached 40 lb. weight. Since growth curves were available for each animal this was readily done (see Graph 1). For litter size 8, period B began when the pig reached 80 lb., and period C when it reached 120 lb. For litter size 9 on the other hand, the end of period A became the beginning of period B, and so on. With the former method there was slight overlapping of periods when more than 40 lb. was put on during the first and second periods. From Table VII it will be seen that the average increase for the second period was $37{\cdot}66 \pm 5{\cdot}54$, so that rather more than a sixth of the pigs were allotted slightly overlapping periods. There is so little difference in the actual growth rates of the second and third periods that this overlapping cannot be of much importance. In both groups, allowances were made for obvious checks in the growth rate to avoid including periods of very slow or no growth. The object was to obtain a fair estimate of the growing capacity and in making any adjustments, the general trend of the growth curve was considered and not any brief periods of fast or slow growth. The checks were by no means confined to the smallest pigs, and sometimes involved whole litters. The post-weaning check was in evidence, but was usually over by the time the pigs reached 40 lb.

A comparison of the means for each period, together with an analysis of the variance is available in Table VII.

The differences between the means of corresponding periods are too small in comparison with the standard deviations to be significant. Litter size may therefore be presumed to have been unimportant here. The most interesting feature of the table is the undoubted significance of the difference between litters in all the periods including the suckling period. In all cases, the chances that the observed differences are purely random are much less than 1 in a 100. Weaning weight, as might be expected, is subject to relatively greater inter-litter differences than the other weight increases. Doubtless they are affected more by seasonal changes than the latter, but allowing for this, an undesirable amount of variation existed in the quality of the sows.

Table VII may lead to the supposition that litters could be easily distinguished. Obviously litter mates must tend to resemble each other more than they resemble non-litter mates, or else there would be no

Table VII. *Mean weaning weight and increases in weight in pounds per pig during three 28-day periods for 29 litters of 8 pigs and 31 litters of 9, together with corresponding analyses of variance*

Litter size 8

		Weaning weight (w)		Period A (x)		Period B (y)		Period C (z)	
Means		$27{\cdot}1 \pm 4{\cdot}98$		$25{\cdot}24 \pm 4{\cdot}52$		$37{\cdot}66 \pm 5{\cdot}54$		$42{\cdot}00 \pm 6{\cdot}16$	
Variance	D.F.	Sw^2	Mean square	Sx^2	Mean square	Sy^2	Mean square	Sz^2	Mean square
Total	231	11,465	49·6	5,566	24·1	8,322	36·0	11,377	49·3
Between litters	28	6,417	229·2	1,422	50·8	2,094	74·8	3,668	131·0
Within litters	203	5,048	24·8	4,144	20·4	6,228	30·7	7,709	38·0
F (1% point about 1·8)			9·2		2·5		2·4		3·4

Litter size 9

Means		$28{\cdot}20 \pm 5{\cdot}58$		$25{\cdot}85 \pm 5{\cdot}09$		$33{\cdot}75 \pm 6{\cdot}23$		$40{\cdot}31 \pm 6{\cdot}97$	
Variance	D.F.	Sw^2	Mean square	Sx^2	Mean square	Sy^2	Mean square	Sz^2	Mean square
Total	278	14,475	52·1	9,002	32·4	14,540	52·3	18,509	66·6
Between litters	30	6,757	225·2	2,572	85·7	4,911	163·7	6,459	215·3
Within litters	248	7,718	31·1	6,430	25·9	9,629	38·8	12,050	48·6
F (1% point about 1·8)			7·2		3·3		4·2		4·4

inter-litter differences, but that the degree of resemblance is not very strong follows from the intra-class correlations calculated from Table VII. The coefficients being small, indicate that within litters the pigs did not vary much less than all pigs regardless of litter. They are as follows:

	Intra-litter correlations based on			
		Increase during period		
Litter size	Weaning weight	A	B	C
8	+0·50	+0·15	+0·15	+0·23
9	+0·40	+0·20	+0·26	+0·27

An exception should be made of the correlations based on weaning weight from which it is apparent that there was a fairly considerable resemblance between litter mates. Such correlations bring out clearly the difficulties with which selection for growth rate is faced. Even if it could be arranged that all pigs in a litter had the same weaning weight, their subsequent growth to bacon weight, under conditions similar to those at Edinburgh, would still yield an intra-litter correlation of the order 0·15 (Smith & Donald, 1937).

Influence of weaning weight on subsequent growth.

The question now arises whether the later differences are associated with the initial differences established by weaning weight. Correlation

coefficients expressing the degree of relationship have therefore been calculated and are shown in Table VIII.

With one exception, the correlations between weaning weight and the weight increases during any of the three periods were insignificant. The exceptional case is difficult to understand, since it indicates the existence of a correlation between weaning weight and the increase in period B (litter size 8), although apparently the first and third periods were independent of weaning weight. Since the correlation between the means of the litters is fairly large, although itself insignificant, some adventitious association of means for weaning weight and increase in

Table VIII. *Correlation between weaning weight and increase in weight during three periods defined by initial weight*

(Litter size 8, 232 pigs; litter size 9, 279 pigs)

Weaning weight and increase in weight during	Calculated from	Litter size 8	Litter size 9
Period A	All pigs	−0·057 N.S.	−0·065 N.S.
	Litter averages	−0·204 N.S.	−0·004 N.S.
	Pigs within litters	+0·035 N.S.	−0·103 N.S.
Period B	All pigs	+0·172 S.S.	−0·020 N.S.
	Litter averages	+0·299 N.S.	−0·097 N.S.
	Pigs within litters	+0·104 N.S.	+0·031 N.S.
Period C	All pigs	+0·079 N.S.	−0·101 N.S.
	Litter averages	+0·264 N.S.	−0·253 N.S.
	Pigs within litters	−0·060 N.S.	+0·001 N.S.

N.S. non-significant; S.S. significant at 1% point.

period B may have contributed enough to the total covariance to make a significant correlation. The signs of the coefficients are not consistent, and it must be concluded that these data contain no satisfactory evidence that either litters or pigs showed a growth rate which was influenced by their weaning weights. As can be seen from the variance of the means, the range of average weaning weights was rather large, and should have been adequate to discover any reasonably substantial effect.

Relation between the increases in weight in different periods.

Under this heading in the previous section it was observed that the correlation between the mean increases in the second and third periods was of the order of 0·6. With the restricted data available for this section, it has been possible to extend the correlation to the individuals within the litters, and to determine how far the observed differences in period B account for the differences in period C. This has been done by

adjusting the variance of the increases in period C in accordance with the covariance of the increases in periods B and C after the manner of Fisher (1936). In this way an estimate of the residual variance in weight increase in period C freed from the effects of the existing variation in period B was obtained.

The adjusted sums of squares for the total variance and the variance within litters for period C were not substantially different from the unadjusted values, but the variance between litters was reduced by about one quarter. The interdependence of the increases in periods B and C is described by the correlation coefficients given in Table IX.

Table IX. *Coefficients of correlation between increases during periods B and C*

	Litter size 8	Litter size 9
All pigs	+0·163 S.	+0·335 S.S.
Pigs within litters	+0·038 N.S.	+0·279 S.S.
Litter averages	+0·477 S.S.	+0·444 S.
No. of litters	29	31

From this Table it may be concluded that the differences between litters in the third period arose largely in that period and were not foreshadowed accurately by the increases in the second period. There was, nevertheless, a distinct tendency for increases in the two periods to be associated. To judge by the correlation coefficients, there was a stronger association between the litter means for the two periods than between the individual weight increases. In fact, when the increases were calculated from a constant weight, as with litter size 8, the latter correlation disappeared just as it did between weaning weight and increase in the first period, calculated from 40 lb. In the group of litters with nine pigs, the third period began where the second ended, and consequently any pig which grew slowly in its second period was handicapped by its small size and absolute growth rate when it entered its third period. The correlation of +0·279 within litters of nine is regarded as having much the same meaning as the correlations between weaning weight and subsequent growth measured from the weaning weight itself.

The correlation between means of litters gives no hint of its origin. It is perhaps rational to suppose that a genetically superior litter in period B may remain genetically superior during period C, but since so little of the variation in C is accounted for by regression of C on B, the weight increases are obviously very susceptible either to a fluctuating

environment, or possibly to the action of hereditary factors just commencing to operate, as, for instance, genes for late or early maturity. The correlations between means of litters given in Table IX, namely, $r=0{\cdot}477$ and $0{\cdot}444$ for litter sizes 8 and 9, may be compared with the corresponding values in Table VI, $r=0{\cdot}50$ for both litter sizes. In spite of the different methods of defining the periods, there is substantial agreement in the estimate of the relation between the increases in weight obtained in the two successive periods concerned.

Discussion

In starting this particular investigation, it was felt that two of the chief difficulties in the way of determining the breeding value of pigs for bacon production were lack of knowledge concerning the sources of variation, and a tendency to regard growth rate, economy of gain or carcass quality, as simple genetic characters with complicated modes of inheritance rather than as complicated characters with components of simple modes of inheritance. Scientific poultry breeding for egg production now consists in the synthesis of genetic factors such as those for egg size, persistency, early maturity and stamina—a system which has proved more satisfactory than breeding on a basis of annual egg numbers. In the same way, the study of milk yield in terms of yields of fat and protein, different types of lactation curve, annual and lifetime productions, is the essence of the present trends of research.

The changes in rate of maturity induced in livestock during their evolution, and the influence of breed in determining age at "finished" weight, permit the inference that the rate and composition of growth are subject to some degree of genetic control. Schmidt *et al.* (1934) demonstrated with breed crosses, and Lush (1936) with the results of Danish progeny testing, that this control is sufficiently variable to offer considerable scope for selection in pigs. In order to make selection more effective, however, some improvement in the judging of genotype from observed performance is urgently required. The improvement may possibly come from a greater degree of subdivision of the growing period. If significant differences in the growth of litters are found in one period which are independent of the differences occurring in a previous period, it may be inferred that genetic differences of the type noted by Berge (1936) and Vecchi (1934) in their breed comparisons are involved. Such an inference is, of course, to be regarded with considerable suspicion until submitted to further experiments designed to test the possibility

that environment is wholly responsible. Genetic variation of this kind, if demonstrated beyond doubt, would be important in investigations of carcass quality and economy of gain.

The decrease of variability observed as the rate of growth increased may be regarded as evidence that equal environmental stimuli do not have equal effects on the growth rate of at least some of the animals. Under the system of group feeding practised, it is inevitable that some pigs will have secured a greater share of the rations than some of their litter mates, but if quantity of food is the principal factor governing the rate of increase, it is probable that when the litter, as a whole, is growing rapidly differences in food consumption will have a smaller effect than would the same differences in a more slowly growing litter. In other words, those animals which are growing at or near their maximum rate respond less to stimuli in either direction than those which are still far from the maximum. Comparable results were obtained by Donald (1937) with suckling pigs which did not show at all levels of nutrition equal increments of weight for equal increments of milk. This relation between variability and growth rate may conceivably come to have some importance, for genetic variation may be most marked at levels of feeding which are not optimal for the production of best quality carcasses.

In a previous paper it has been shown (Smith & Donald, 1937) that weaning weight has a very definite influence on the subsequent rate of growth of bacon pigs, as measured from time of weaning. This is entirely in agreement with the published observations of many workers in various countries. It was pointed out in the same paper, however, that the resemblance in growth rate of pigs of the same weaning weight (as measured by intra-class correlation) was very slight. This was taken to mean that weaning weight considered without relation to other factors, such as the weights of litter mates, was a poor guide to subsequent performance. Similar conclusions have been arrived at by Husby (1933), Wenck (1931), Berge (1936), Schmidt & Zimmermann (1934) and Menzies-Kitchin (1937). That the ordinary correlation between weaning weight and subsequent growth is more a statistical than a biological conception can be demonstrated by defining the subsequent growth periods by initial weight instead of initial age. In the preceding pages, both methods have been used. The former yields no significant correlation, while the latter does. The difference is due to the inclusion in the calculations by the latter method of the time necessary for the light weaners to put on the deficient weight at weaning at an age when they are growing comparatively slowly. This is probably the reason why his correlations

of weight at different ages did not allow Axelsson (1933) to support the suggestion of Bengtsson (1929) that the growth rates of a pig, before and after 20 kg. in weight, were independent. Berge (1936) observed a small correlation of $+0{\cdot}139 \pm 0{\cdot}040$ between the two rates, a result which, taken in conjunction with the present results, suggests that Bengtsson (also Dunlop, 1933) was substantially correct. Regarded in this light, the correlation between weaning weight and subsequent performance as usually computed, becomes a measure of the extent to which pre-weaning environment (principally milk production in relation to sow and nipple) affects age at slaughter weight. Such a correlation may be justifiably used for deductions concerning the environment of young pigs but not the pigs themselves. Under certain conditions, some modification of this interpretation requires to be made. If the assumption cannot be made that light pigs incur no permanent injury to their powers of growing, then some degree of correlation between weaning weight and subsequent growth calculated in either fashion is to be expected. In general, the numbers of such pigs in herds with weaning weights averaging 30 lb. or more will be rather few.

Summary

1. The post-weaning growth of 135 litters has been analysed with a view to determining the relationship of certain arbitrary subdivisions with each other. For this purpose, the weight increases during three periods of 28 days have been defined in two ways—first, by age, the periods being 10–14, 14–18, and 18–22 weeks, and secondly, by weight, the periods beginning at 40, 80 and 120 lb. and continuing as before for 4 weeks.

2. When the periods are defined by age, the mean increase per pig per litter is affected by weaning weight, but not by litter size (Table III). The variability of the individual increases becomes greater as the pigs become older and heavier (that is, passing from one period to a later one), but less within a period as the rate of growth increases (Table IV). It was not affected by litter size.

3. The distribution of individual weights became increasingly skew with age. This is regarded as a graphical illustration of the fact that while absolute rate of growth is increasing, initially small animals must fall farther and farther behind (Graph 3).

4. The correlations between the average litter increases in different periods were calculated for litter sizes 6–11. In general, the coefficient

for periods 1 and 2 was about 0·4, and for periods 2 and 3 about 0·6 (Table VI). This is interpreted to mean that, when judged by results over the whole time under observation, litters with a high correlation between the increases in weight during short periods are not properly comparable with those with a low correlation. By this method, differences in rate of growth having an important influence on carcass quality may be obscured.

5. Since the correlations of the total increase during all three periods with those during the second and third periods were scarcely affected by removing the effect of the increase in period 1, it is concluded that, under Shothead conditions, the weights of the pigs at 10 weeks are too low to ensure that post-weaning checks are avoided. A more reliable test would be obtained by considering only the growth from the second period onwards, that is, from 14 weeks old.

6. When the periods are defined by weight, differences between litters in amount of weight put on in 28 days are still significant in each of the three periods (Table VII). Differences in weaning weight were more marked than the differences in subsequent growth.

7. No effect of weaning weight on subsequent growth during the periods defined by initial weight was observed.

8. The correlation between the average litter-increases for the second and third periods was 0·47 for litters of eight and 0·44 for litters of nine. The corresponding figures for the periods defined by age were 0·50 and 0·50. These comparatively low correlations suggest that careful control of environment in testing stations is necessary for reliable litter testing, and that results from such stations should be examined for evidence of genetic differences in rate of growth during restricted portions of the total test period.

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INFLUENCE OF AGE AND WEIGHT OF PIGS ON RESPONSE TO SODIUM EVIPAN

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Young pigs (large white breed) are favourable subjects on which to study the relation between dosage and body weight because they weigh about 1 kgm. at birth and rise to 80 kgm. within 6 months. The range of weight is similar to that which covers the growth of human beings. The experiments described below were made to determine firstly the susceptibility to a quick-acting barbiturate of new-born pigs and secondly the relation between dosage and body weight. The former point is of practical interest in relation to the use of barbiturates in obstetrics and the latter point is of importance as regards basal narcosis in children.

The literature relating to barbiturates is too extensive to permit full references, but comprehensive reviews have been compiled by Lundy (1) and by Levy (2). The following special points are relevant to our experiments. Holck et al. (3) showed that adult male rats were more resistant than female rats to quick-acting barbiturates, but showed no sex difference in response to slow acting barbiturates. No sex difference was found with other animals (dog, cat, rabbit, guinea pig). Tolerance to repeated administration of pentobarbital was noted by Moir (4) and Carmichael and Posey (5). No sex difference was observed in the young pigs and we endeavoured to avoid establishment of tolerance by allowing at least 7 days' interval between injections.

As regards the relation between dosage and body weight in adult animals Mulinos (6) using amytal on cats found that large animals were more resistant than small ones. Bazett and Erb (7) found the reverse to be true of pentobarbital given to cats and

dogs. They found also that fat animals were more resistant than thin animals. As regards the relation between age and dosage, Pearcy and Weaver (8) found that young dogs were more resistant than adult dogs to sodium barbitone. Carmichael and Posey (5) found that large guinea pigs were more susceptible than small ones to pentobarbital; Moir (4) and Carmichael (9) found the same to be true for rats. Holck et al. (3) found that adult male rats were more resistant to sodium evipan than young rats whilst adult females were slightly less resistant.

The evidence is therefore conflicting and inconclusive as regards the relative susceptibility of infants and of adults to barbiturates. As regards the dosage of sodium evipan for pigs Reichwald (10) found that doses of about 20 mgm. per kilogram given intravenously produced narcosis in pigs between 25 kgm. and 90 kgm. weight.

EXPERIMENTAL METHODS

Seven litters (50 animals) of large white pigs were studied between January and March 1938. Sodium evipan was administered intravenously by the ear vein. A constant dose of 20 mgm. per kilogram (10 per cent solution) was given. This always produced full narcosis. After a certain time the animals endeavoured to regain their feet, and the duration of action was measured from the time of injection until the animals were able to stand. Care was taken to keep the animals warm with hot water bottles during the period of narcosis.

Injections were commenced with new-born pigs and continued at intervals of 1 or 2 weeks until the pigs were about 3 months old. A few other experiments were made on gilts and castrated males from 3 to 6 months old.

RESULTS

Figure 1 shows that new-born pigs (2 to 4 days) are more susceptible than older pigs to sodium evipan and also show a very wide scatter in their response. Pigs 8 and 9 days old are slightly more susceptible than older pigs, but there is no demonstrable difference between pigs 2 weeks old (weight 3 kgm.) and pigs

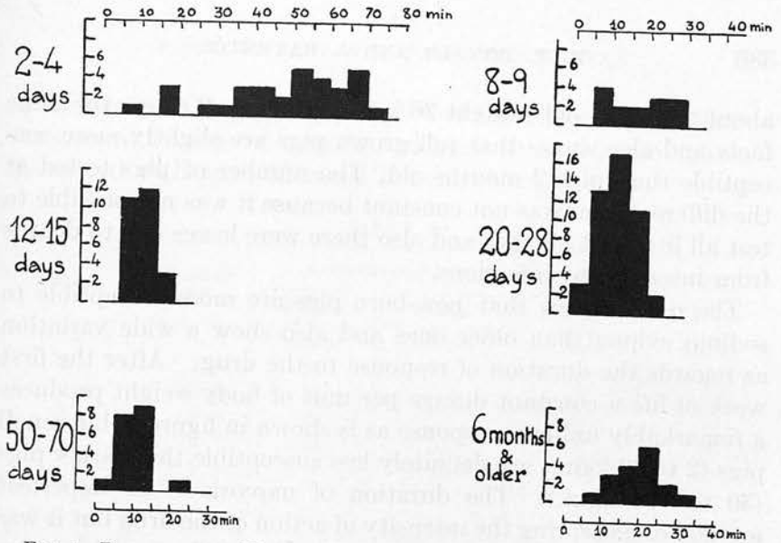

FIG. 1. DURATION OF NARCOSIS PRODUCED BY 20 MGM. PER KILOGRAM SODIUM EVIPAN (INTRAVENOUS) IN PIGS OF VARYING AGES

Ordinates: number of pigs; abscissae: duration of narcosis in 5 minute intervals.

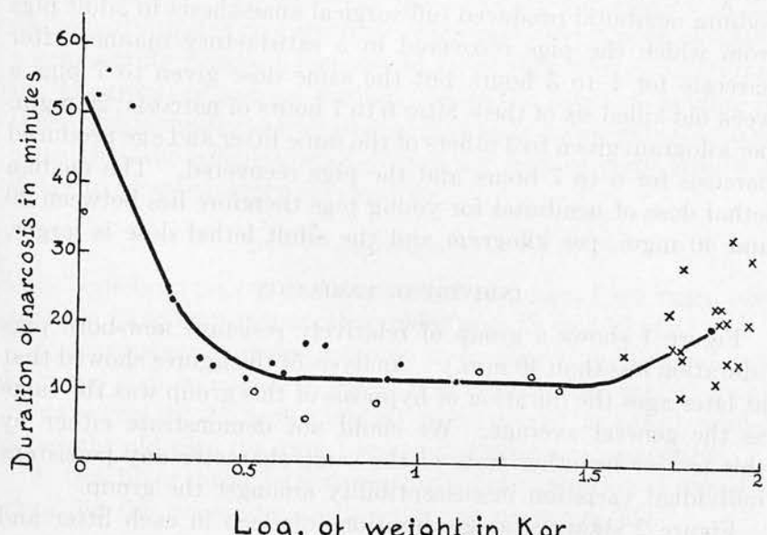

FIG. 2. RELATION BETWEEN BODY WEIGHT AND DURATION OF NARCOSIS PRODUCED IN PIGS BY 20 MGM. PER KILOGRAM SODIUM EVIPAN (INTRAVENOUS)

Ordinate: duration of narcosis; abscissa: log. body weight in kilogram; dots: average response of litters; circles: average responses of most resistant litter (no. 3); crosses: responses of individual adult pigs.

about 2 months old (weight 20 kgm.). Figure 2 shows the same facts and also shows that full grown pigs are slightly more susceptible than pigs 2 months old. The number of pigs tested at the different ages was not constant because it was not possible to test all litters at all ages and also there were losses due to deaths from intercurrent infections.

The results show that new-born pigs are more susceptible to sodium evipan than older ones and also show a wide variation as regards the duration of response to the drug. After the first week of life a constant dosage per unit of body weight produces a remarkably uniform response as is shown in figure 2, but small pigs (2 to 30 kgm.) are definitely less susceptible than larger pigs (30 to 100 kgm.). The duration of narcosis is an imperfect method of measuring the intensity of action of the drug but it was not practicable to determine the median lethal dose. This value was determined approximately in the case of sodium nembutal (intramuscular injection). A dose of 40 mgm. per kilogram of sodium nembutal produced full surgical anaesthesia in adult pigs from which the pigs recovered in a satisfactory manner after narcosis for 4 to 5 hours, but the same dose given to 7 pigs a week old killed six of these after 6 to 7 hours of narcosis; 20 mgm. per kilogram given to 3 others of the same litter and age produced narcosis for 6 to 7 hours and the pigs recovered. The median lethal dose of nembutal for young pigs therefore lies between 20 and 40 mgm. per kilogram and the adult lethal dose is larger.

INDIVIDUAL VARIATION

Figure 1 shows a group of relatively resistant new-born pigs (duration less than 40 min.). Analysis of the figures showed that at later ages the duration of hypnosis of this group was the same as the general average. We could not demonstrate either by this test or by other tests of the same character any persistent individual variation in susceptibility amongst the group.

Figure 2 shows average durations of sleep in each litter and there is a considerable variation. Table 1 shows that the sensitivity of different litters differed consistently. For example litter 3 showed at several ages the shortest average for the duration of sleep. The average weights of this litter were similar to the general average of weights and hence this resistance was not associated with any difference in general health.

TABLE 1

LITTER	NUMBER OF PIGS	AVERAGE DURATION OF SLEEP AT VARIOUS AGES IN DAYS			
		2–4 days	8–9 days	12–15 days	20–30 days
		minutes	*minutes*	*minutes*	*minutes*
1	7	56		14	14
2	10	51		12	13
3	9	35		10	6
4	10	53	15		17
5	6		23		17

DISCUSSION

Our results show that new-born pigs are more susceptible to barbiturates and also show a much wider variation in response than older animals. This indicates the necessity for caution in the use of barbiturates in obstetrics. Pigs more than a week old show a remarkably constant response to a constant dosage (milligram per kilogram) of sodium evipan. Since the range of weights of these pigs is similar to the range of human body weights this indicates that the calculation of dosage per unit of body weight is likely to be satisfactory for children.

SUMMARY

1. New-born pigs (2 to 4 days old; 1 to 2 kgm.) are more susceptible to sodium evipan than older pigs (2 to 30 kgm.).

2. A constant narcotic response is produced by 20 mgm. per kilogram sodium evipan in young pigs between the ages of about 10 days (weight 2.6 kgm.) and 80 days (weight 20 kgm.), whilst 6 months old pigs (64 kgm.) are somewhat more susceptible.

3. One litter showed a consistently shorter duration of narcosis than did the remainder, during the first month of life.

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THE VARIATION IN LENGTH OF INTESTINE IN NEWLY HATCHED CHICKS

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The problems of efficiency of food utilization and growth rate are now receiving attention in most domestic animals and are studied in the face of the serious difficulty that little is known of the anat--omical and physiological differences between appar--ently similar animals. Under the circumstances, variation in performance under identical conditions cannot be ascribed to any particular cause, nor can it be inferred from equal performance that the animals involved are anatomically and physiologically uniform. Just as it has been found necessary in the investigation of carcass quality and milk yield to analyse the economic character into its component parts, so will it be necessary to consider efficiency and rate of gain as the end results of a long chain of processes, the links of which are the real subject of enquiry.

The study of variation in the performance of very young animals which is the general subject of a research programme at this Institute must take account of the fact that all animals are not born equal. Since their response to environment after birth must be affected thereby, the nature and extent of the inequality assumes considerable importance. An obvious possibility is that under some conditions of feeding the length and surface area of the intestine may influence the digestion and absorption of food. A

number/

number of investigations dealing directly or indirectly with the subject of intestine length have been carried out, mainly on rodents, and reference to them will be made elsewhere. Pilz (1937) discusses the specific characters of the intestine in domestic poultry, but the work of Riddle is of more moment for the present purpose. That work established a sex difference in the weight of the pituitary gland of adult ring doves and pigeons which was associated with a sex difference in intestine length such that the females within each species had heavier pituitary glands and longer intestines than the males (Riddle and Flemion, 1928; Riddle and Nussman, 1933). This was followed up by the demonstration that the administration of prolactin causes the overgrowth of the liver and intestines (Bates, Riddle, Lahr, and Schooley, 1937). Whether the differences in intestine length found in newly hatched chicks forming the material for this report can be explained on endocrinological grounds is a question which must be disregarded here. The possibility of a sex difference on the other hand does fall within its scope which is to discover the amount of variation in intestine length occurring naturally in newly hatched chicks and not accounted for by differences of sex or body weight.

Material and Methods.

Material and Methods

During March and April of 1937, successive hatchings of Brown Leghorn chicks produced for other purposes then discarded, were available for the first part of this investigation. Since the chicks were discarded only after hatching was completed, it follows that the description 'day-old' includes chicks varying from about 1 to 36 hours old. For the second part of the work, a further 109 chicks of the same breed were specially hatched from two settings in September 1938. These were subdivided into groups which will be described in detail later.

All chicks were weighed alive to the nearest gram then killed. The gut was carefully dissected out, laid out straight with slight stretching to show up any regions still restricted within the mesentery, and measured to the nearest millimetre. Lengths of intestine from gizzard to yolk-sac and from yolk-sac to cloaca were recorded as well as total length. With the exception of the first few chicks, the gonads were inspected to determine sex.

Results

Mean weights and lengths of intestine for the first 6 groups of chicks are given in Table 1. The most striking feature of the data is the difference between the first two and the later groups. The obvious explanation of the lower weight and longer intestines of /

of the two early groups is that they were older than the later groups when killed and had consequently lost weight but continued to grow in respect of the length of the gut. Excluding these, there were, owing to the uniformity among the other groups, no reasons to suppose that they were not simply samples from the same population. Analyses of variance have been made to test the significance of differences among group means and between sex means, but in no case could such differences be established statistically. Tests were also made to determine whether the variability of the females was greater than that of the males, but again real differences could not be found.

Table 1

Average live weights and lengths of intestine in day-old Brown Leghorn chicks

Group	No.		Mean weight in gr.		Mean length of intestine in cm.					
					Total		Stomach to yolk-sac		Yolk-sac to cloaca	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
1	25		37.7		44.6		24.2		20.4	
2	40		38.8		47.4		26.6		20.8	
3	26	24	42.2	40.5	41.2	44.2	22.8	24.5	18.4	19.7
4	8	11	43.1	41.4	43.1	42.8	23.6	23.6	19.5	19.2
5	11	8	39.8	41.0	44.3	41.2	24.5	22.8	19.8	18.4
6	13	18	42.4	42.2	41.9	41.0	23.0	22.7	18.9	18.3
3-6	58	61	41.9	41.2	42.2	42.6	23.3	23.6	18.9	19.0
S.D.			3.6	3.5	3.5	4.1	1.9	2.4	2.1	1.9
C.V.(%)			8.6	8.5	8.3	9.5	8.3	10.0	11.1	9.7

C.V., coefficient of variability; S.D.,standard deviation.

In many papers presenting data on intestine length coefficients of variability are given, and for the sake of comparison, these are appended to Table 1. The values were about 9% for both live weight and length of intestine, and indicate a moderate degree of variability. As Day and Fisher (1937) have pointed out, the use of coefficients of variability for comparison of variabilities involves the assumption that in general variation is such that changes in means are accompanied by proportional changes in standard deviations - an assumption which is often not permissible and need not be made if sufficient data are available to make analyses of the covariance of means and their standard deviations. Any comparison therefore, of the variability in live weight or length of intestine of day-old chicks with that of older birds should take account of this fact.

Relation between live weight of chick and length of intestine

Graphical representation of the relation between live weight and total length of intestine revealed that if any regression existed it was slightly negative. This unexpected result was borne out by the subsequent analysis of covariance shown in Table 2. The analysis ignored the original groups which were not distinguishable in any way, but recognized sex.

The sums of products (-32.5 and -165.6) are small in comparison with the corresponding sums of squares/

squares, so that the derived regression sum of squares is also small. Among the females, the portion of the variance accounted for by regression (37.4) falls well short of significance since the ratio 37.4/16.05 does not reach the required value of 4.0. Among the males the variance due to regression (1.4) is negligible, so that on these data the live weight of a chick is no indication of the length of its intestine.

The relation between the two parts of the intestine on either side of the attachment of the yolk-sac was apparent on inspection and seemingly closer for the females than for the males. The statistical evidence given in Table 2 brings substantiation in respect of all the birds grouped simply according to sex, the regression sum of squares being many times larger than the error mean square. Within each of the original subgroups 3-6 however, the same sex difference existed.

Table 2

Tests of significance of regression

	W^2	WL	L^2	Regr. sum of squares	Adjusted sum of squares	D.F.	Mean square	b
♂♂	734.7	- 32.5	696.5	1.4	695.1	56	12.4	-
♀♀	732.7	-165.6	984.5	37.4	947.1	59	16.1	-
	$YS-C^2$	(YS-C) (G-YS)	$G-YS^2$					
♂♂	253.6	113.9	214.3	51.2	163.1	56	2.9	+0.45
♀♀	205.2	224.7	329.9	246.0	83.9	59	1.4	+1.09

W, live weight ; L, total length ; YS-C, yolk-sac to cloaca; G-YS, gizzard to yolk-sac; b, regression coefficient.

The values of the regression coefficients in Table 2 show that in the females an increase of 1 cm. in the length of the posterior part of the intestine was accompanied by a nearly equal change in the length of the anterior part. In the males there was apparently less similarity in the rates of development of the two parts since an increase of 1 cm. in the posterior part meant a change of only 0.45 cm. in the anterior part. The difference between the two regressions, namely 0.64 has a standard error of 0.14 and is therefore significant by the usual standards. As neither this result nor the virtual absence of a relationship between live weight and length of intestine were expected, it was deemed advisable to repeat the observations on a material more closely controlled as to age after hatching.

Second series of observations on intestine length

Two lots of approximately 100 eggs each were set at an interval of a week. Fifty to sixty chicks from each were expected over a period of hatching of 36 hours. When hatching began, the chicks were watched until one third (18-2o) were out, and these were then weighed and ringed, and allotted at random to three subgroups (a) for immediate killing, (b) for killing after 24 hours, and (c) for killing after 48 hours. Subgroups (b) and (c) were then returned to the incubator. About 12 hours later when another third of the chicks were hatched the same procedure was gone through, and again when the last/

last chicks used had hatched 24 - 36 hours from the beginning. Thus for each lot of eggs set, there were 9 subgroups of chicks, but since only age after hatching was of interest, the six (a)'s have been combined in the calculations, and similarly the (b)'s and (c)'s. All chicks were therefore weighed and numbered within 12 hours of hatching. Those killed immediately after weighing were approximately 6 hours old on the average, the next to be killed about 30 hours old (6 plus 24 hours), and the last about 54 hours old. No food or water was offered.

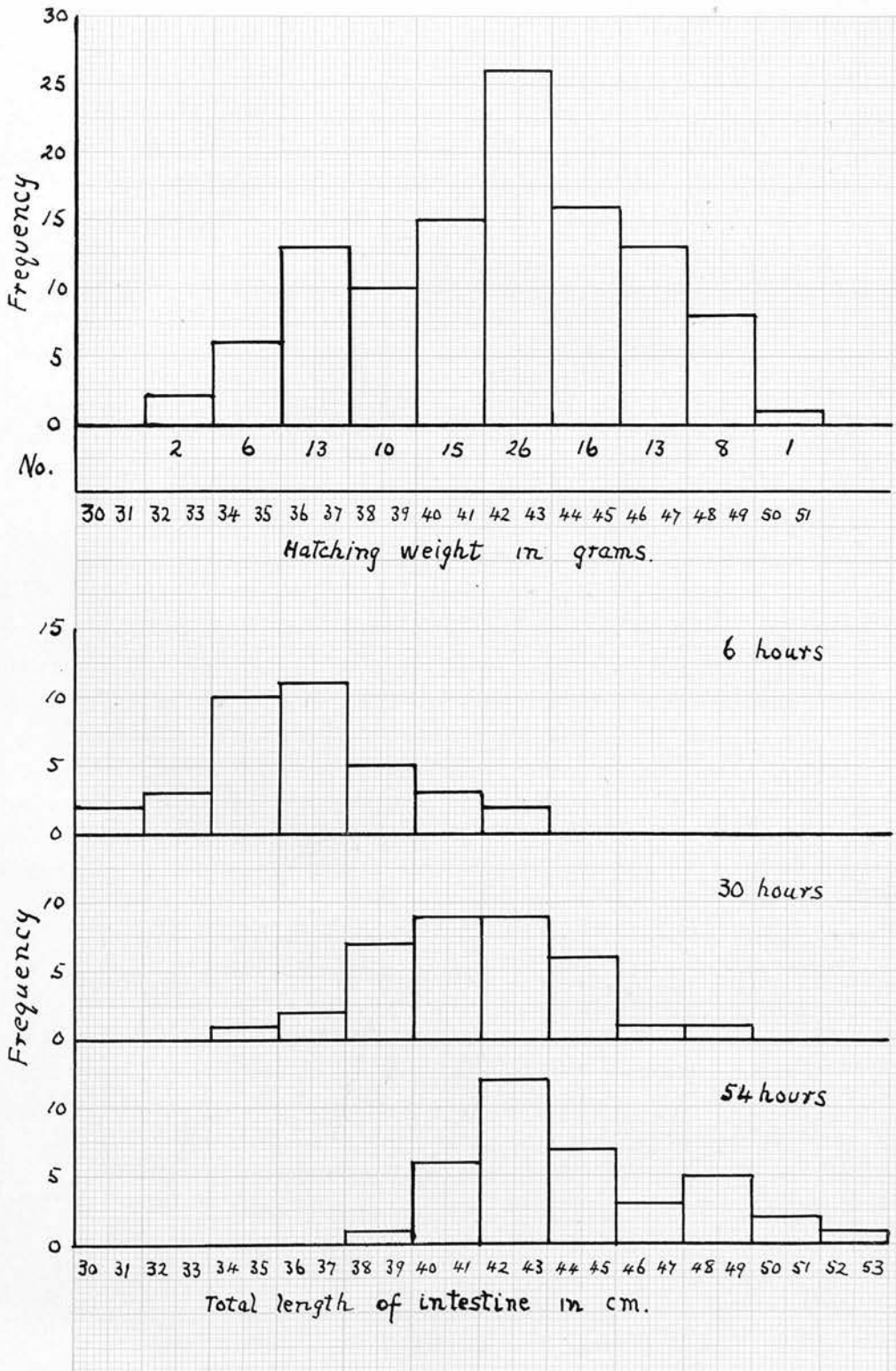
When killed the chicks were weighed again, and dissected as before, except that the weight of the yolk-sac was recorded in addition to sex and lengths of intestine.

Table 3 contains the means of the various observations grouped according to age after hatching.

Table 3

Means of observations on chicks killed at varying ages after hatching. Weights in gr. and lengths in cm.

Age (hours)	Sex	No.	Weight at hatching	Weight when killed	Weight of yolk sac	Length of intestine		
						Total	G-YS	YS-C
6	♂♂	13	43.5	42.5	7.2	38.0	20.7	17.3
	♀♀	23	41.8	41.0	7.5	35.7	19.2	16.5
30	♂♂	16	41.7	37.5	4.2	42.5	23.2	19.3
	♀♀	20	41.7	37.5	5.1	40.9	22.9	18.2
54	♂♂	22	43.2	36.5	3.0	45.3	25.2	20.1
	♀♀	15	40.9	34.4	3.7	43.1	23.9	19.2



Graph 1. Frequency distributions of hatching weight and total intestine length.

of significance made in Table 4 indicate that as before males have the same weight as the females. But contrary to the experience of the first series of observations there now appears a sex difference in intestine length, both of the parts and the whole. Romanoff (1933) has observed a similar difference in total length but does not say whether or not it was statistically significant. Riddle and Flemion (1927) also found a sex difference in doves, but it was the females and not the males which had the longer intestines. These measurements were made on adult birds.

Table 4

Tests of significance of effect of sex on weight (in gr.) at time of killing, and on intestine length (in cm.).

Source of variation	D.F.	Weight when killed		Length of intestine					
				Total		G-YS		YS-C	
		MS	F	MS	F	MS	F	MS	F
Sex within age groups	3	7.9	-	36.2	4.1	11.4	3.5	7.7	3.7
Within sex and age groups	103	12.4		8.8		3.3		2.1	

MS, mean square deviation; F is the ratio of the mean square deviations (Snedecor, 1934). Values of F greater than 3.09 indicate significance at the 5% point when the degrees of freedom (D.F.) are 3 and 100.

Closer control of age having brought a sex difference to light, the relation of live weight and intestine length has been studied in each each sex and age group separately and combined. From the variance and /

and covariance of the two variables, six estimates of the regression of total length on live weight were obtained which although not individually significant yielded a combined value which was significant at the 1% point. The coefficient and its error proved to be+0.22 ±0.08, so that in general each 1 gram increase in the live weight of the chicks was accompanied by an increase of 0.22 cm. in the total length of intestine.

As shown by the values of the coefficient for each of the 6 subgroups, however, there was much variation in the intensity of the association of weight and length.

Table 5

Regression coefficients

Age in hours	Sex	No.	Regression of total length of intestine on		Regression of length from Gizzard to yolk sac on length from yolk-sac to cloaca
			Live weight	Live weight less weight of yolk-sac	
6	♂♂	13	-0.16	+0.12	+0.64
	♀♀	23	+0.18	+0.29	+0.74
30	♂♂	16	+0.08	+0.06	+0.56
	♀♀	20	+0.38	+0.54	+0.99
54	♂♂	22	+0.32	+0.42	+1.07
	♀♀	15	+0.39	+0.45	+0.92
all ♂♂		51	+0.14	+0.26	+0.81
all ♀♀		58	+0.27	+0.41	+0.87
all chicks		109	+0.22	+0.35	+0.84
standard error			+0.08	+0.09	+0.09

The tendency for the coefficients to grow larger as the chicks became older may have had some connection with the fact that the chicks heavy at hatching lost relatively more weight from the yolk-sac than the lighter chicks. If this were the case, then the relation of live weight and intestine length would be greater than that represented by a regression coefficient of +0.22 which is based on total live weight . Re-calculating the regression coefficient from live weight less weight of yolk-sac leads to the value of + 0.35 ± 0.092. This although larger, is not significantly different from +0.22, hence the rather low values of the regression cannot be attributed to variable quantities of yolk. That these values are low can be inferred from the extent of the reduction in the variation of intestine length when body weight is held constant. By doing so, the original variance, 8.8, is reduced by only 6% to 8.3 when the effects of total body weight are eliminated, and by 11% if variation in weight of yolk-sac is also eliminated.

Whatever the factors which control the weight of chicks at hatching, they would appear from these data to exert very little influence over the growth in length of the intestine up to that time. As a result the digestive apparatus of newly hatched chicks is far from being equivalent even in those of the same weight.

As far as the sex difference in the relation of the two parts of the intestine is concerned, the evidence in the last column of Table 5 suggest that the previously observed sex difference arose from conditions of sampling

which were not repeated in the second series of observations. Table 5 shows that over all chicks of this latter series the regression within sex and age groups is estimated at 0.84. Thus for each increase of 1 cm. in the length of the intestine from yolk-sac to cloaca, there was a corresponding increase in length from gizzard to yolk-sac of 0.84 cm. By taking this fact into account, the variation in the length of the section from gizzard to yolk-sac was reduced by about 42%. The remaining 58% yields a coefficient of variability of 8%.

It will have been noted that the values of the regression coefficient again increase with the age of the chicks (as did those for live weight and total length) becoming comparable with those found for females in the first series of observations. Those observations were made on chicks of roughly the same age as those in the 30 and 54 hour groups of the second series, which suggests that hatching may be followed by the assumption of a more uniform rate of growth of the gut than occurred before hatching. The sex difference in the strength of the resemblance in length of the two portions of the intestine found at first now becomes explicable if it is supposed that the male chicks tended to hatch later than the females. This tendency may be seen in the second series also. Although on this evidence it may be concluded that in general both portions of the gut were/

were lengthening at much the same rate, more than half the variation in the length from gizzard to yolk-sac remained unaccounted for by variation in length from yolk-sac to cloaca.

Discussion.

According to Galpin (1939), hatching weight bears very little relation to the subsequent growth rate of chicks from the same flock as those used in this study. This is quite in keeping with what is known of the relation between birth weight and subsequent growth in mammals, and it follows that embryonic growth, conditioned as it must be by the nutritional status of the embryonic environment, may have little or no value in forecasting growth response in a completely different environment. After birth or hatching, respiration and nutrition undergo radical changes for which the young animals are not equally adapted. It is apparent from the data now presented that unless the naturally occurring variation in length of intestine is of no significance in the digestion and absorption of food, some chicks will begin eating solid food with an advantage over other chicks of the same weight but with a different length of intestine. In more general terms, it may be stated as a point of view, that it is not body weight at any time which is of importance during the succeeding phase of growth but the relative sizes and rates of functioning of the parts of the body. All attempts to explain differences in growth/

growth rate must then be ultimately concerned with that organ or part which sets the upper limit to growth rate. The geneticist looking for heritable differences in food utilization and growth rate, and the nutritionist searching for improved diets are both concerned with this since the efforts of both will be seriously hindered until the fundamental causes of the unequal performance of apparently similar animals in a similar environment are known.

The objections to the use of live weight as an index of growth receive an addition from the special case of the day-old chick. Here the reserve of nutriment in the yolk-sac permits growth of the intestine and probably of other organs and tissue as well although the live weight is clearly diminishing. In spite of the loss of weight, the capacity of the chicks to grow is not impaired since those tissues in which a check to growth might have permanent ill effects are protected by the yolk. In place of yolk, deposits of fat probably serve the same purpose in those animals which possess them.

Acknowledgement.

The author wishes to acknowledge his indebtedness to Dr. A.W.Greenwood for extending the necessary facilities for this work.

Summary

(1) The length of intestine in over 200 newly hatched chicks has been considered in relation to sex and live weight.

(2) The coefficient of variability in chicks of mixed ages up to 36 hours old was 9%. When age after hatching was more closely controlled, this value was reduced to 7%.

(3) During the first 48 hours after hatching, the chicks lost 6-7 gr. weight, but in the same time the intestine increased in length by 7 cm.

(4) Males were of the same weight as the females but had significantly longer intestines.

(5) There was a slight tendency for heavy chicks to have longer intestines than light chicks, but the amount of variation accounted for by differences in live weight amounted to only 11%.

(6) The yolk-sac divides the intestine into two parts the lengths of which are positively correlated. The variation in the length of the anterior part was reduced by 42% when correction was made for the length of the posterior part.

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GROWTH RATE AND CARCASS QUALITY IN BACON PIGS

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The interpretation of carcass reports from bacon factory graders must have a restricted value until satisfactory working limits are set to the amount of variation in carcass quality which may arise from uncontrollable variations in growth rate at any time during the course of ordinary pig feeding practice. Total points awarded on the basis of numerous measurements are of course of little genetical value, but taken individually many of the customary measurements may be valuable if the nature of their variation is known and understood. Carcass quality measurements, from the breeders' point of view, are made from an unsatisfactory standpoint. Instead of measurements being taken as a result of the knowledge that there are genetical differences arising from segregation of Mendelian factors, the breeder has been made conscious of the suitability or otherwise of his pigs according to certain criteria of the bacon manufacturer, and the problem has thus become one of determining to what extent variations in measurements according to these criteria have a genetical basis. It is obvious from breed differences and wide crossing experiments that certain generalized qualities such as rate of maturity, length, and leanness are genetically conditioned. This is/

is, however, not of any great importance to the owner of a given breed who wishes to know how important genetical differences are within the limits of his own and similar herds.

Material suitable for determining whether the results of a carcass examination can be seriously affected by such common fluctuations has become available from the Large White herd of the University of Edinburgh, pigs from which have been subjected to carcass measurements through the courtesy and assistance of the Bacon Development Board of Great Britain. The measurements are discussed in this paper and are essentially those mentioned in the method for judging pork and bacon carcasses by Davidson and others (1). The six measurements concerned have been examined in relation to four measures of growth rate, namely, weaning weight (at 8 weeks); live weight increase (L.W.I.) during the 2 months directly following the time each pig reached 40 lb. weight, the live weight increase (L.W.I.) during the month directly preceding the time each pig reached 210 lb.; and the average daily gain in weight calculated from the age at slaughter and the cold carcass weight. The second and third of these/

these measures of growth rate have been obtained from individual graphs based on fortnightly weighings.

The total number of pigs was 44, distributed in six litters. Direct analysis of variance of each of the 10 variables led to the results given in Table 1, in which the values of F exceeding 2.46 may be regarded as evidence that the means of the 6 litters showed significant differences.

Table 1 (see following page).

Thus, of the measures of growth, only weaning weight showed real litter differences. Here the individual variation was low compared with the variation of the means, whereas in the other measures the opposite was true. Of the carcass measurements, loin length, maximum thickness of fat at the shoulder , and thickness of back fat at the level of the last rib, showed significant litter differences, whereas leg length, thickness of fat over the middle of the rump muscle, and breadth of eye muscle at end of last rib did not.

The next step was to determine whether these carcass measurements were associated in any way with changes in the growth rate. This was done by determining the regression coefficients and the significance of/

Table 1

Results of direct analysis of variance of all variables. The analyses are represented only by the mean squares within litters and F, the ratio of the mean square between litters to the mean square within litters. In each analysis, $n_1 = 5$, and $n_2 = 38$, for which the 1% and 5% values of F are 3.54 and 2.46 respectively.

Independent variable (pounds)	Mean square within litters	F	Dependent variable (mm.)	Mean square within litters	F
Weaning weight	18.7	4.35 SS	Loin length	422	2.54 S
L.W.I. in two months after reaching 40 lb.	157	NS	Leg length	223	2.19 NS
L.W.I. in one month before reaching 210 lb.	58.9	1.40 NS	Max. thickness of fat at shoulder	13.6	3.06 S
Average daily L.W.I.in carcass weight	2587	1.83 NS	Thickness of fat at end of last rib	8.7	3.03 S
			Thickness of fat at middle of rump muscle	17.0	1.86 NS
			Breadth of eye muscle at end of last rib	21.7	1.61 NS

S, significant at the 5% point ; SS, significant at the 1% point ; NS, non-significant.
Note : The analysis of average daily live weight increase in carcass weight has been made with coded data involving multiplication and therefore is comparable only with the corresponding mean square in Table 3.

of regression variance within litters from the analysis of variance and covariance in the usual way. (Fisher 1936). The results appear in Table 2.

Table 2 (see following page).

With the exception of loin length, the carcass measurements were apparently uninfluenced by fluctuations in the growth rate variables. Loin length, however, was definitely affected by rate of growth immediately before reaching 210 lb. in such a way that the faster growing animals were shorter than the slow growing animals at slaughter. This graphically obvious tendency over all the pigs within litters was also expressed by the means of litters and within nearly all the individual litters. This somewhat surprising result is, however largely accounted for by the fact that the slower growing pigs were killed at a heavier weight than the fast growing animals. As will be shown elsewhere, the variation in cold carcass weight affects leg and loin length but not thickness of fat or breadth of eye muscle, so far as the present data are concerned.

The/

Table 2

Coefficients of regression (R) and significance of regression variance. For $n_1 = 1$, and $n_2 = 37$, the 1% and 5% points of F are 7.37 and 4.11 respectively.

Dependent variable (mm.)	Independent variable in pounds									
	Weaning weight			L.W.I. in 2 months after reaching 40 lb.			L.W.I. in one month before reaching 210 lb.			Average daily gain in carcass weight (coded)		
	R	F		R	F		R	F		R	F	
Loin length	-1.364	3.33	NS	-0.734	9.30	SS	-0.998	5.97	S	-0.101	2.49	NS
Leg length	0.109		NS	-0.111		NS	-0.419	1.80	NS	-0.044		NS
Max. thickness of fat at shoulder	0.025		NS	0.037		NS	0.105	1.87	NS	0.009		NS
Thickness of fat at last rib	0.044		NS	0.023		NS	0.100	2.68	NS	0.015	2.77	NS
Thickness of fat at mid-rump muscle	-0.119		NS	0.023		NS	-0.048		NS	0.005		NS
Breadth of eye muscle at last rib	0.197	1.30	NS	-0.003		NS	0.059		NS	0.015	1.01	NS

The next question is whether adjustment of carcass measurements to allow for variation in the growth rate variables will affect the significance of the differences between the litter means as given in Table 1. Making such adjustment according to Fisher's method leads to the results of Table 3, in which the significance of the unadjusted litter differences is indicated in brackets.

Table 3 (see following page).

As might have been expected, loin length differences are those chiefly affected. Adjustment for weaning weight causes no changes, but elimination of the other growth rate variables has removed the original significant litter differences. Of the other carcass measurements, only one shows a change in significance, namely, thickness of fat at the shoulder, which is no longer significant when adjusted for weaning weight.

Since the litters comprised varying numbers of males and females, it is of interest to know whether results similar to those just described would be found within each sex. Analyses of the unadjusted variances disclosed very clear differences between the sex means in three of the variables, loin length (SS), thickness of fat at the shoulder (SS), and thickness of fat at the/

Table 3

Significance of litter differences when adjustment is made for initial variation in the independent growth rate variables. For $n_1 = 5$, and $n_2 = 37$, the 1% and 5% values of F are 3.56 and 2.47 respectively.

Dependent variable (mm.)	Values of F, adjustment being made for :			
	Weaning weight	L.W.I. in two months after reaching 40 lb.	L.W.I. in one month before reaching 210 lb.	Average daily gain in carcass weight
Loin length	3.37 S (S)	2.22 NS (S)	1.66 NS (S)	2.33 NS (S)
Leg length	1.56 NS(NS)	2.17 NS (NS)	1.93 NS (NS)	2.24 NS (NS)
Max. fat at shoulder	2.07 NS (S)	2.63 S (S)	2.78 S (S)	3.14 S (S)
Fat at last rib	2.85 S (S)	3.36 S (S)	2.86 S (S)	3.18 S (S)
Fat at mid-rump muscle	1.21 NS(NS)	1.79 NS (NS)	1.88 NS (NS)	1.78 NS (NS)
Width of eye muscle at end of last rib.	1.59 NS(NS)	1.57 NS (NS)	1.60 NS (NS)	1.68 NS (NS)

The significance of the differences between litter means when no adjustment is made is shown in brackets. S, significant at the 5% point; SS, significant at the 1% point; NS, nonsignificant.

the level of the last rib (8), the males being shorter and fatter. On anlysis of covariance and of the adjusted variance, the observed regression variance within sexes and the variance of the adjusted sex means were insignificant in respect of leg length, thickness of fat the mid-rump muscle and breadth of eye muscle. In the other three carcass measurements, the sex differences remained significant, and the results in respect of regression variance within sexes were the same as were found previously within litters, with one exception. Within sexes but not within litters thickness of shoulder fat showed a significant amount of negative regression on weaning weight.

The relative importance of heredity and environment in causing variations in carcass measurements will naturally vary with the degree of genetic similarity of the pigs concerned. Since all the litters here described were by the same boar and were all born within two weeks of each other, genotypical and seasonal elements in their variation should have been at a comparatively low level. Results the same as those here presented are therefore not necessarily to be expected with other groups of pigs. Within this

rather/

rather homogeneous sample, environmentally induced variations of the stated kinds have had slight if any observable effect on carcass quality. These variations are considered representative of those commonly occurring in bacon pig production with the exception of weaning weight which has been rather low.

Summary.

(1) Standard measurements on the carcasses of 6 litters of bacon pigs (44 animals) all sired by the same boar have been examined in relation to growth rate as determined by the weight at weaning, by increases in weight during the first 2 months after weaning and during the month before slaughter, and by the average daily gain in carcass weight.

(2) Significant differences between litters were found in respect of weaning weight, loin length, thickness of fat at the shoulder, and thickness of fat at the end of the last rib.

(3) Significant sex differences were observed in loin length and thickness of fat at the shoulder and last rib, the males being shorter and fatter than the females.

(4) No satisfactory evidence has been found that the thickness of back fat, breadth of eye muscle, or leg length characteristic of litters has been seriously affected by the litter differences in growth rate during certain specified periods.

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GROWTH RATE AND CARCASS QUALITY IN BACON PIGS

A STUDY OF POLYNOMIAL COEFFICIENTS FITTED TO GROWTH RATE DATA

BY

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GROWTH RATE AND CARCASS QUALITY IN BACON PIGS

A STUDY OF POLYNOMIAL COEFFICIENTS FITTED TO GROWTH RATE DATA

By H. P. DONALD

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(With One Text-figure)

Recent experiments have shown that plane of nutrition exerts an influence on carcass quality (Mansfield *et al.* 1937; McMeekan & Hammond, 1939). It therefore becomes of importance to know how far carcass reports may be affected by variations in the growth rate of pigs arising under the customary pig-rearing conditions of the industry, whether they be due to temporary loss of appetite, to climatic or other environmental fluctuations, or to the action of differing gene combinations. Apart from the desirability of knowing to what extent carcass quality can be controlled after a pig is born, the need for improved methods of judging genotype from recorded measurements of carcasses requires that non-genetic variation should be carefully estimated and allowed for.

In a previous paper (Smith & Donald, 1939) the presence of extensive variation in the growth rate of pigs and whole litters during 28-day periods of their lives was discussed, and it was shown that under conditions of feeding which were as uniform as possible, without taking uneconomic precautions to control environment, the growth of litters in any period is not a reliable indication of subsequent performance. It follows that many litters growing comparatively quickly after weaning may be growing comparatively slowly in the later stages of fattening, and vice versa. The possibility that these facts concerning growth rate might be related to carcass quality has been studied in a group of forty-four animals all by the same boar, and farrowed within a fortnight (Donald, 1939). Since the sows were also interrelated, the genetic variance in these pigs should have been less than that obtaining in a random sample, and non-genetic variance therefore relatively more important. The variation in thickness of back fat and breadth of eye muscle, however, did not appear to be caused by differences in rate of growth as measured by increases in weight during various periods of the pigs' lives.

This study, being based on growth rates or gains calculated from initial and final differences in weight of a stated period, may have been hindered by some inaccuracy in estimating growth rate in this way. The work has therefore been extended to include the fitting of cubic curves to the data obtained from the fortnightly weighings during the growing period in the manner suggested by Wishart (1938, 1939). Such fitted curves may be regarded as describing the growth of the pigs more satisfactorily than the actual weights, because intermediate weighings can be utilized, changing rates of growth can be simply specified, and irregularities arising from the weighings of live pigs are smoothed out.

In this paper a second group of thirty-one pigs (five litters by three boars) unrelated to the first group of forty-four pigs, has also been considered.

METHOD OF ANALYSIS

The object has been to describe as briefly as possible the growth rate of the pigs from weaning onwards, but in such a way that changes in the rate were not merged into a single average. This was done by calculating orthogonal polynomials to the third degree according to the method of Aitken (1933). Logarithms of the live weights were used in the hope of minimizing the significance of the cubic term, and of avoiding undue emphasis on the variation in gains of live weight which may occur in the latter stages of fattening. To simplify the calculations, eleven weights for each pig in group I, and ten for each pig in the faster-growing group II were used. The last was obtained at the final regular fortnightly weighing before dispatch to the bacon factory. Working backwards from this, ten (or nine) more consecutive weights were taken, which meant that the average age of a pig at no. 1 weight was 10–12 weeks. An example of the calculation of the coefficients, and the test of their significance is given in Table I.

This particular example was not typical, but was chosen to illustrate a case in which the cubic term was large, and reference to the actual weights or to Fig. 1 (*a*) will indicate that this has arisen from a period following weaning in which apparently little growth took place. Fig. 1 (*b*) shows the actual and fitted growth curves for a pig more closely resembling the average animal. As shown by Aitken, the fitted values for each weighing can be readily calculated from the data in Table I. If the differences between these fitted values (Y) and the actual recorded values (y) are squared and summed, the value of $S(Y-y)^2$ obtained is the same as that remaining after the mean and the three coefficients have been

Table I. *Example of the fitting of a cubic curve and the testing for significance of the polynomial coefficients*

No.	x	Live weight lb.	Log	100 (log − 1·5)	S_1	S_2	S_3	S_4
1	−5	54	1·73	23	*581*			
2	−4	57	1·76	26	558	*3632*		
3	−3	56	1·75	25	532	3074	*11962*	
4	−2	80	1·90	40	507	2542	8888	*25108*
5	−1	94	1·97	47	467	2035	6346	
6	0	116	2·06	56	420	1568	4311	
7	1	130	2·11	61	364	1148	2743	
8	2	151	2·18	68	303	784	1595	
9	3	170	2·23	73	235	481	811	
10	4	190	2·28	78	162	246	330	
11	5	217	2·34	84	84	84	84	84

($Sy^2 = 35589$)

Terminal values and differences of Tchebychev polynomials ($n = 11$)

	a_0	a_1	a_2	a_3
581	1	−5	15	−30
3632		1	−9	36
11962			2	−20
25108				5
	11	110	858	4290

$$a_0 = \frac{581}{11} = 52{\cdot}81$$

$$a_1 = \frac{3632 - 5\,(581)}{110} = \frac{727}{110} = 6{\cdot}61$$

$$a_2 = \frac{2\,(11962) - 9\,(3632) + 15\,(581)}{858} = \frac{-49}{858} = -\,0{\cdot}057$$

$$a_3 = \frac{5\,(25108) - 20\,(11962) + 36\,(3632) - 30\,(581)}{4290} = \frac{-378}{4290} = -\,0{\cdot}088$$

Progressive elimination of regression variance

Degree k	a_k	Numerator	Product	$S(Y-y)^2$	D.F.	Mean square	Significance of reduction in variance
—	—	—	—	35589			
0	52·82	581	30688	4901	10	490·10	
1	6·61	727	4805	96	9	10·67	S.S.
2	−0·057	− 49	2·8	93·2	8	11·65	N.S.
3	−0·088	−378	33·3	59·9	7	8·56	N.S.

Significance of cubic term: $F = 33{\cdot}3/8{\cdot}56 = 3{\cdot}89$, which is non-significant, the 5% point being 5·59 for $n_1 = 1$ and $n_2 = 7$.

fitted as in the last part of Table I (in that example, 59·9). For the majority of the pigs the residual sum of squares lay between 10 and 30, which represents a mean square of 1·5–4·3, or a standard deviation of about 1·2–2·1 or 2–4% per observation. Since they are based on logarithms, these values are not directly applicable to the actual weights.

For the purposes of this study, the formation of regression equations was not considered necessary. But to show the relation of the coefficients to the actual changes in growth rate, the basic form of the equation may

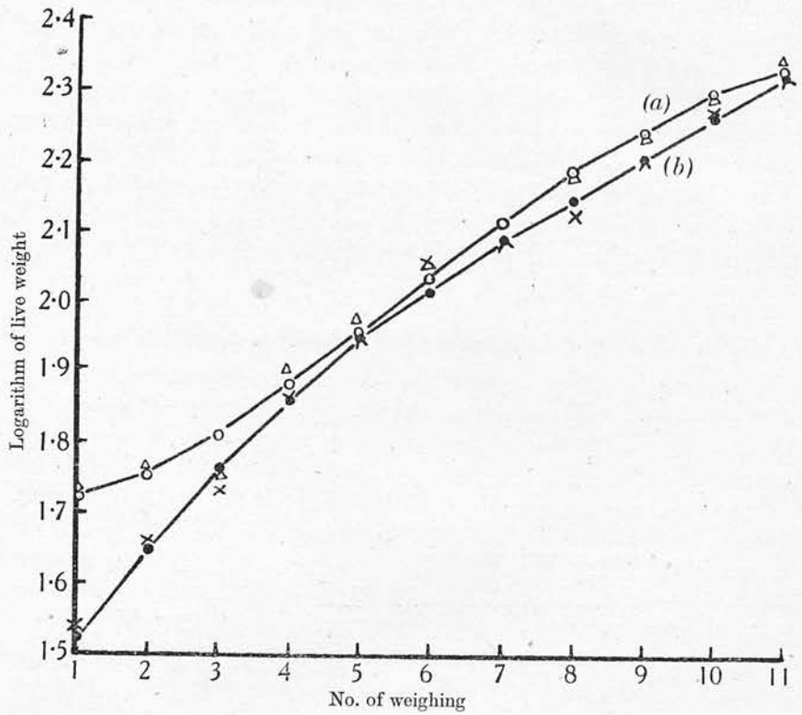

Fig. 1. Observed and fitted values of the logarithms of live weights of two pigs.

	(a)	(b)
a_0	+52·81	+47·82
a_1	+ 6·61	+ 7·62
a_2	− 0·057	− 0·350
a_3	− 0·088	+ 0·039

Observed values △——△ ×——×
Fitted values ○——○ ●——●

be written down from the table of terminal values and differences as shown by Aitken, thus (for $n=11$):

$$Y=a_0+a_1(x-5)+a_2\left[\frac{2x(x-1)}{1.2}-9x+15\right]+a_3\left[\frac{5x(x-1)(x-2)}{1.2.3}\ldots\right],$$
$$=a_0+a_1(x-5)+a_2[(x-5)^2-10]+a_3[\ldots],$$

where Y is the estimated weight of a pig at a given time x. Since a constant number of weighings was used for the pigs of each group, the

terms following the a coefficients are the same in each group. The growth rates of the pigs may therefore be compared by means of the a coefficients alone. The mean of all the weighings is a_0. The average rate of growth, or the slope of the straight line fitted to the weights is represented by a_1 and the rates of change in growth rate by a_2. Since the weights are in the form of logarithms, a_2 represents changes in the relative rate of growth with increasing age.

Since some variation in the cold carcass weight was unavoidable, it has been thought advisable to introduce carcass weight (w) as an extra variable in order that the relation of carcass measurements to growth rate could be determined free of complications arising from that source. Moreover, the use of the a coefficients as the sole measures of growth is open to the objection that if weaning weight were correlated with them, any effects of pre-weaning growth would be inseparable from those associated with the coefficients representing post-weaning growth. Weaning weight (h) as a further independent variable was therefore included.

The carcass measurements (in mm.) selected for study were (a) loin length as from the first rib to the edge of the *symphysis pubis* bone; (b) leg length as from the latter point to the tip of the toe of the hindleg; (c) maximum thickness of fat at the shoulder; (d) thickness of fat at the level of the last rib; (e) thickness of fat over the middle of the rump muscle; and (f) breadth of eye muscle. With the exception of (f) the measurements were taken from both sides of the split carcasses and averaged for each pig; (f) was measured after curing from three rashers cut from one side at the level of the last rib.

Results

Table II shows the mean values for the fitted coefficients. In each group the hogs made faster growth than the gilts (a_1), but the rate slowed up more towards bacon weight (a_2), the downward curvature of the fitted line at its upper end being greater the larger the negative value of a_2.

Owing to the different numbers of weighings in the two groups, the average performance of each must be compared by means of the appropriate equations which are:

Group I $Y=14{\cdot}58+9{\cdot}79x-0{\cdot}306x^2$,

Group II $Y=11{\cdot}50+11{\cdot}70x-0{\cdot}420x^2$.

Table II. *Mean values of a coefficients, cold carcass and weaning weights (in lb.), and carcass measurements (in mm.) for groups I and II*

Group	a_0	a_1	a_2	a_3	Cold carcass weight (w)	Weaning weight (h)	No. of pigs
I. Hogs	51·6	6·97	−0·337	0·041	152	27·2	20
Gilts	53·8	6·53	−0·280	0·023	157	27·3	24
All pigs	52·8	6·73	−0·306	0·031	155	27·3	44
II. Hogs	50·7	4·19	−0·908	−0·013	158	29·7	15
Gilts	53·5	3·75	−0·785	−0·002	159	32·1	16
All pigs	52·2	3·96	−0·845	−0·007	159	31·0	31

	Length of		Thickness of fat at			Breadth of eye muscle
	Loin	Leg	Shoulder	Last rib	Mid-rump muscle	
I. Hogs	766	572	53·3	33·7	32·8	45·8
Gilts	788	573	49·1	31·6	31·2	47·7
All pigs	778	572	51·0	32·6	31·9	46·8
II. Hogs	783	585	53·6	31·9	33·7	47·1
Gilts	794	590	51·2	30·3	31·4	47·0
All pigs	789	587	52·4	31·1	32·5	47·1

The curve for group II was therefore steeper than that for group I (x), but showed greater curvature (x^2). This difference in curvature was probably due to the necessity of slowing up in the second group the growth of pigs waiting for fortnightly slaughterings. For present purposes, the difference in growth rate between the groups is advantageous since it increases the range of growth rates over which the following investigations apply. This range, in terms of the age at time of last weighing was 200–302 days for group I and 181–229 days for group II, and in terms of the weight put on during the 22 (or 20) weeks prior to slaughter was 132–188 lb. for group I, and 153–189 lb. for group II.

The fitting of a_0 and a_1, and of a_2 (with three exceptions) always significantly reduced the variance. Of the a_3 coefficients, thirty-six out of forty-four in group I and eleven out of thirty-one in group II were positive, and the rest negative. The fitting of eleven (ten positive) in group I, and of two (both negative) in group II, brought about a significant reduction in variance. Nevertheless, the a_3 coefficients derived from these logarithmic data were so small and variable in sign that they were thenceforth disregarded. Further, little interest attached to a_0, and attention was therefore fixed on a_1 and a_2.

Direct analyses of variance established sex differences in a_1, but not a_2. As reported previously (Donald, 1939), sex differences were found in the carcass qualities: loin length, thickness of fat at the shoulder and thickness of fat at the level of the last rib, males being shorter and fatter than females. In what follows, therefore, variances and covariances have been calculated within sexes so that the regressions of carcass measurements on the a coefficients represent the weighted averages of the corresponding regressions for hogs and gilts. Litter differences were small and have been neglected. The analysis has thus been directed towards determining whether the observed variations in the carcass measurements within sexes were related to the variations in the corresponding coefficients a_1 and a_2, taking into account the cold carcass weight, and weaning weight.

The method of multiple regression given by Fisher (1936) and Snedecor (1938) was adopted. The calculation of c multipliers rendered the following calculations very simple and rapid. For each of the six carcass measurements the total correlations with the four independent variables were required from which to calculate the standard partial regression coefficients. As an example the procedure for loin length is given in Table III. For the other carcass measurements the same c multipliers were used, but each time with the appropriate set of four correlation coefficients. The standard partial regression coefficients are independent of units of measurement, and may be used to compare the

Table III. *Estimation of standard partial regression coefficients for loin length (b) in relation to a_1, a_2, w, and h*

	b	a_1	a_2	w	h
Sum of squares	16,083	2605	7908	2130	1118
Sum of products:					
ba_1, ba_2, etc.		−1359	1848	2405	− 24
a_1a_2, a_1w, etc.			−1811	− 518	− 67
a_2w, etc.				− 334	−174
wh					−494
Correlation coefficients:					
r_{ba_1}, r_{ba_2}, etc.		−0·21	+0·16	+0·41	−0·01
$r_{a_1a_2}$, etc.			−0·40	−0·22	−0·04
r_{a_2w}, etc.				−0·08	−0·06
r_{wh}					−0·32

Solving:

$$\begin{aligned} c_1 - 0{\cdot}40c_2 - 0{\cdot}22c_3 - 0{\cdot}04c_4 &= 1\ 0\ 0\ 0 \\ -0{\cdot}40c_1 + c_2 - 0{\cdot}08c_3 - 0{\cdot}06c_4 &= 0\ 1\ 0\ 0 \\ -0{\cdot}22c_1 - 0{\cdot}08c_2 + c_3 - 0{\cdot}32c_4 &= 0\ 0\ 1\ 0 \\ -0{\cdot}04c_1 - 0{\cdot}06c_2 - 0{\cdot}32c_3 + c_4 &= 0\ 0\ 0\ 1 \end{aligned}$$

Solution	1	2	3	4
c_1	=1·3300,	+0·5780,	+0·4088,	+0·2186;
c_2	=0·5780,	+1·2662,	+0·2899,	+0·1918;
c_3	=0·4088,	+0·2899,	+1·2526,	+0·4348;
c_4	=0·2186,	+0·1918,	+0·4348,	+1·1595;

whence the standard partial regressions

$$\beta_{ba_1 \cdot a_2wh} = c_1 r_{ba_1} + c_2 r_{ba_2} + c_3 r_{bw} + c_4 r_{bh} = -0{\cdot}0178 \text{ (solution 1)};$$
$$\beta_{ba_2 \cdot a_1wh} = c_1 r_{ba_1} + c_2 r_{ba_2} + c_3 r_{bw} + c_4 r_{bh} = +0{\cdot}2042 \text{ (solution 2)};$$
$$\beta_{bw \cdot a_1a_2h} = c_1 r_{ba_1} + c_2 r_{ba_2} + c_3 r_{bw} + c_4 r_{bh} = +0{\cdot}4739 \text{ (solution 3)};$$
$$\beta_{bh \cdot a_1a_2w} = c_1 r_{ba_1} + c_2 r_{ba_2} + c_3 r_{bw} + c_4 r_{bh} = +0{\cdot}1576 \text{ (solution 4)}.$$

relative importance of a_1, a_2, w (cold carcass weight), and h (weaning weight), as factors in the variation of the carcasses. Thus Table III shows that the partial regression of loin length on carcass weight ($\beta_{bw} = +0{\cdot}4739$) was more than twice as great as that of loin length on either a_1, a_2 or h.

The partial regressions now available were used to estimate the total correlation (R) from the formula

$$R^2 = r_{ba_1} \cdot \beta_{ba_1.a_2wh} + r_{ba_2} \cdot \beta_{ba_2.a_1wh} + r_{bw} \cdot \beta_{bw.a_1a_2h} + r_{bh} \cdot \beta_{bh.a_1a_2w}.$$

R^2 sums up in a convenient way the proportion of the total variance which is accounted for by the dependence of the carcass measurements on the four variables a_1, a_2, w and h. What is left ($1-R^2$) of the total variance represents variations in carcass quality still uncontrolled. The significance of R and thus of the reduction in variance due to correction for multiple regression may be read off the appropriate tables (Snedecor, 1938).

The standard partial regression coefficients were also tested for significance separately. For example, the coefficient $\beta_{bw.a_1a_2h} = +0{\cdot}4739$ had a variance of $\frac{1-R^2}{\text{D.F.}} . c_{33}$, the square root of which was $\pm 0{\cdot}1591$. The coefficient was therefore 2·98 times its standard error, and significant at the 1% point (D.F. = 38).

A summary of the calculations for all the carcass measurements is given in Table IV.

Table IV. *Standard partial regression coefficients* (*n* = 44 *in group I and* 31 *in group II*)

		Length		Thickness of fat			Breadth of eye muscle
	Group	Loin	Leg	Shoulder	Last rib	Mid-rump muscle	
a_1	I	−0·02	−0·30†	+0·06	+0·24	+0·06	−0·01
	II	+0·25	+0·02	+0·03	+0·03	+0·43†	−0·14
a_2	I	+0·20	+0·02	+0·07	+0·20	−0·07	−0·21
	II	−0·27	+0·29	+0·01	+0·09	+0·09	−0·31
w	I	+0·47*	+0·52*	+0·18	+0·11	+0·13	+0·08
	II	+0·26	+0·55*	+0·38†	+0·46*	+0·29	+0·03
h	I	+0·16	+0·40*	−0·27	−0·06	−0·23	+0·19
	II	+0·25	+0·42*	−0·24	−0·75*	−0·28	+0·12
R^2	I	+0·23†	+0·47*	+0·14	+0·07	+0·10	+0·08
	II	+0·38†	+0·53*	+0·17	+0·67*	+0·35†	+0·13

a_1, a_2, fitted coefficients; w, cold carcass weight; h, weaning weight.
*, significant at 1% point; †, significant at 5% point.

It is to be borne in mind that the regression coefficients in Table IV refer not to the original units of measurement but to units equal to the

standard deviation of the variables. Thus the coefficient +0·47 for loin length and carcass weight in group I means that when adjustment is made for a_1, a_2 and h, an increase in carcass weight equal to the standard deviation in carcass weight was associated with an increase in loin length of 0·47 of the standard deviation of loin length. Another point to remember is that values of a_2 are negative and therefore the signs of the regression coefficients are affected.

Genetically, the pigs of group I were probably more alike than those of group II. The former were all by the same boar, while the latter were out of sows unrelated to the first lot and by three other boars. Further, group II pigs were 11 mm. longer in the loin than group I pigs, 15 mm. longer in the hindleg, but just as fat along the back. These details of breeding and conformation are of interest in considering the response of each group to the changes in growth rate.

(1) *Loin length.* The values of R^2 show that correction for the four independent variables has resulted in a reduction of "error" variance by one-quarter or more. The sources of the reduction are, however, not equally important in the two groups and consequently it is not possible to predict with assurance what would happen in other samples of pigs. It may be assumed that carcass weight has a real effect on loin length, and probably also weaning weight, because the two coefficients, although not significant, agree reasonably well with each other and in direction with the corresponding coefficients for leg length. The influence of a_1 and a_2 was non-significant in both groups, and therefore small or negligible. The difference between the coefficients for a_2 is rather wide and suggestive of an unlike response by the two groups such that with an increasing rate of decline in relative growth rate, loins became longer in group II than in group I.

Within a limited range of growth rates, loin length seems to depend mainly on body weight and but little on the rate at which that weight was attained. The present figures support those of Mansfield *et al.* (1937), who found that the average loin length of fifty pigs on an unrestricted diet was the same as that of fifty restricted pigs reaching bacon weight 35 days later.

(2) *Leg length.* The evidence here is unmistakeable that weaning weight and carcass weight have modified leg length. Heavy weaners and heavy baconers have had longer legs than light weaners and baconers, and allowance for this fact has resulted in decreasing uncontrolled variation by one-third to one-half. But here too the effects of growth rate are unlike in the two groups.

In group I, short legs have been associated with high values of a_1 (that is, steep growth curves), whereas in group II they have been associated with high negative values of a_2 (that is, curves showing rapid decline in relative growth rate towards the end). McMeekan & Hammond (1939) observed that their fast-growing pigs had a low proportion of head and legs compared with slow-growing pigs, and it might have been expected therefore that the faster-growing group II pigs would have had shorter legs than the slower-growing group I pigs. Reference to Table II will show that the reverse was the case, group II pigs being distinctly leggier in type. Although the data require cautious interpretation, it is interesting to speculate whether the failure of the long-legged group II pigs to conform with those of group I and of McMeekan & Hammond is due to a retention to a greater age of the tendency in both groups for fast growth up to weaning to lead to greater leg length. Such differences as these might be expected in pigs since they are born with short legs that have to undergo a period of rapid growth during which they may readily respond to both genetic and environmental influences. With grazing animals, like sheep and cattle, the new-born have relatively long legs, the growth of which, after birth, is slower and probably less susceptible to modification.

(3) *Thickness of fat at the shoulder.* For this character, the regression coefficients show much uniformity. The rate of growth has been unimportant, but as might have been expected, carcass weight has probably affected the thickness of fat. The coefficients for weaning weight fall short of significance, but since they agree well, it seems likely that heavy weaners developed less shoulder fat. This would be in keeping with the greater growth in length of bone observed in the same pigs, provided more bone meant less fat at constant weight. The reduction in variance achieved has been comparatively small.

(4) *Thickness of fat at the level of the last rib.* There are notable differences here in the behaviour of the two groups of pigs. Group I coefficients for a_1 and a_2, though not significant, agree that there was a tendency for fast growth and thick fat to go together, but in group II the tendency was very slight. Further, both carcass and weaning weight have affected group II very noticeably, but group I hardly at all. The result is that control of variation is very substantial in group II and negligible in group I.

(5) *Thickness of fat above the middle of the rump muscle.* At this point group II pigs have become more susceptible to differences in growth rate (a_1) and group I pigs less so. This, in conjunction with (4) above, suggests

that the two groups were of different types from the point of view of development of back fat. The influence of weaning weight has, however, been similar in both groups as it was for shoulder fat, the heavy weaners developing less fat than the light.

(6) *Breadth of eye muscle.* This character appears to have been resistant to modification by any of the variables studied, for very little control of variation has been secured. The most that can be said is that a slowing up of growth in the late stages of fattening may have been responsible for the observed thickening of the eye muscle in pigs with large negative values of a_2, but the effects have not been great enough to yield statistical significance. Using other variables, Crampton (1938) found variation in this character equally difficult to account for.

(7) R^2. The values of R^2 give the portion of the total variance which arises from the regression of the dependent carcass measurements on the independent variables, a_1, a_2, w and h. Table IV shows that adjustment for these regressions has resulted in a considerable reduction in the observed variance of leg and loin length, and sometimes in the variance of other carcass measurements. In so far as certain numerically large, but non-significant, values of the correlation between pairs of variables are fortuitous, it cannot be assumed that in other samples of pigs equal reductions in variance can be achieved by the same corrections. The present results do show, however, that under some circumstances the corrections may be large enough to influence appreciably the magnitude of the carcass differences between groups of tested pigs which can be detected by statistical methods. They show also that some parts of the carcass are more susceptible to modification than others, but the order of susceptibility is not necessarily the same in distinct strains of pigs.

Loin length and thickness of back fat

Although the main purpose of this study is to circumscribe variation, it is of interest to consider the results in the light of published accounts of carcass quality variation. Judged merely by their statistical results, there is a disconcerting lack of agreement among them. As an example, the relation between loin length and thickness of back fat may be cited. Lush (1936) compared the results of Jespersen and Madsen with his own from Danish pigs, and points out that their correlations of $-0{\cdot}197$ (based on 3577 hogs) and $-0{\cdot}145$ (based on 3382 gilts) are lower than his estimate of $-0{\cdot}39$ (based on the means of 1285 tested litter samples). The reason for the differences between such large samples is not clear, but it may be connected with genetical changes induced in the breeding stock by

selection. Again, in Canada the same correlation calculated by Sinclair & Murray (1935) and by Stothart (1938) for shoulder fat was small and non-significant. These authors emphasize the genetic variability of their pigs, which may have been responsible for obscuring any relationship of loin length and thickness of back fat.

The results obtained from the present data show an interesting difference in Table V, which gives the standard partial regression of back fat at three levels on loin length.

Table V. *Standard partial regression of back fat on loin length.* (*a*) a_1, a_2 *and carcass weight held constant;* (*b*) *carcass weight and weaning weight held constant*

	Shoulder	Last rib	Mid-rump muscle
(*a*) Group I	−0·58	−0·49	−0·37
Group II	−0·16	−0·10	−0·19
(*b*) Group I	−0·50	−0·45	−0·35
Group II	−0·06	+0·09	+0·06

Group I exhibits a much closer dependence of back-fat thickness on loin length than does group II. This contrast between the groups cannot be attributed to the shape of the last 20–22 weeks of the growth curve, nor to differences in weaning weight or carcass weight. But genetic differences in conformation might account for the discrepancy. At a constant weight, long and short carcasses cannot have the same conformation, but the difference may not always be expressed in the same way. Thus in some strains extra length brings thinner back fat; in others it may bring thin bellies or narrow sides.

DISCUSSION

The value of the statistical technique of fitting polynomial coefficients to growth records can hardly be judged fairly until more is known of the physiological nature of growth. There are various ways of describing a growth curve and their usefulness depends on their suitability for the purpose in hand. The simple method of calculating differences between initial and final weight is open to objections, including its failure to take previous history into account. Similarly the more sophisticated fitting of curves of any kind to serial data may entail neglect of some essential fact in spite of giving a very accurate description of the observed changes. The use of total live weight as a measure of growth is probably unsound in quantitative studies of body tissues, since it is a composite of the changing weights of all tissues and organs, each of which has its own rate

of development. Nevertheless, an animal exists as a unit, so that there must be harmony and integration of its component parts and its internal functioning. The fact that a pig retains to a considerable degree its power to express its own type and develop true to an inborn pattern under diverse conditions, is the external expression of this internal regulation.

To appreciate the remarkable resilience of animals to changing conditions, one need only think of the experiments of McCay *et al.* (1935) and Jackson (1936, 1937), who found that rats subjected to long periods of arrested growth by under-feeding while still young, later attained almost normal body size and proportions when adequately fed. In experiments of a somewhat similar nature with pigs, however, McMeekan & Hammond (1939) observed that extreme differences in plane of nutrition did affect the proportions of bone, muscle and fat in the resulting carcasses. Compared with the treatments which were necessary to produce them, the differences obtained may not appear very great, but from the point of view of carcass quality, they were most important. The question which this study set out to answer was whether or not the growth rate differences and changes in groups of pigs raised for bacon in the customary way had affected carcass quality. As far as these pigs are concerned, the answer is that growth rate did affect carcass quality, but that the extent of its effects varied with the part of the carcass, with the time at which the growth rate was measured, and with the genetical constitution of the pigs. Thus, good growth up to weaning has favoured bone and muscle growth at the expense of fat in the carcass, and fast growth after weaning, though of no importance in several measurements, has influenced others in the direction of more fat and less muscle.

So far as they go, therefore, these results agree with the conclusion of McMeekan & Hammond, that maximum leanness in pigs destined for bacon is obtained by securing rapid growth while the pigs are young, and by limiting the rate of growth (and therefore the rate of fat deposition) as they approach bacon weight.

As a factor in the control of variation in carcass quality, however, growth rate would appear to become rapidly less important than other factors (such as hereditary differences in type and conformation) as the extremes of growth rate approach each other. This applies, of course, to conditions of rearing in which both hereditary and environmental influences on the growth and development are at work. When hereditary variation is limited and environmental variation emphasized, as in the Cambridge experiments, the effects of the latter may be expected to be more clearly defined.

Reference to the foregoing tables will show that differences between individual measurements provided the bulk of the variation even when growth rate and carcass weight were held constant. The position would appear to be, therefore, that while hereditary type is likely to be the principal factor in carcass quality, animals deviating from the ideal may be modified towards it by adjusting the rearing conditions. Experience with the relationship of loin length and back fat, however, points to the need for caution in applying the results with any given strain of pig to pigs in general, for it seems possible that the response to raising or lowering the plane of nutrition may not be the same in pigs which are naturally unlike in conformation.

SUMMARY

1. An examination of carcass reports from two groups of bacon pigs (comprising eleven litters and seventy-five pigs) was made to determine whether the variation in growth rate of normally reared pigs was associated with differences in carcass measurements. The method adopted was to fit orthogonal polynomials to the third degree to the last 10–11 fortnightly weighings converted to logarithms.

2. The residual standard deviation after fitting was about 2–4%. For present purposes, the fitting of second degree parabolae appeared adequate.

3. By means of standard partial regression coefficients, the dependence of each of six carcass measurements on growth rate (a_1), rate of change of growth rate (a_2), carcass weight, and weaning weight, was determined. Both loin and leg length tended to increase as weaning and carcass weights increased, but the response to variations in a_1 and a_2 was neither marked nor consistent in the two groups, possibly owing to a difference in type. Thickness of shoulder fat was negatively correlated with weaning weight, but unaffected by variation in a_1 or a_2. Thickness of fat at the level of the last rib was very responsive to differences in weaning weight in one group, but not in the other, while over the middle of the rump muscle the degree of dependence on weaning weight was about the same in both groups. A tendency was observed for fast growth after weaning and thick back fat to be associated, but this was shown by one group above the last rib, and in the other over the rump muscle. Breadth of eye muscle appeared to be largely independent of all the variables, although in both groups a tendency falling short of significance was found for the muscle to become thicker as the rate of decline of relative growth rate towards bacon weight increased.

4. Statistical control of variation in carcass measurements by adjustment for regression on the four independent variables was greatest for loin and leg length (amounting to a reduction in variance of about one-quarter to one-half) and least for shoulder fat and breadth of eye muscle for which it did not reach the level of significance. The adjustments applied to thickness of fat at last rib and mid-rump muscle were very small and non-significant in one group, and substantial and significant in the other, reaching 67% for thickness over the last rib.

5. The dependence of thickness of back fat on loin length was strong in one group and weak in the other. The difference is probably genetic in origin, and suggests an explanation for the discrepancies among published results.

6. Since the influence of growth rate on carcass measurements appears to have been expressed in a variable way according to type of pig concerned, it may be unwise to make detailed predictions of the relation between growth rate and carcass quality.

The difficulty of establishing effects of growth rate after weaning on carcass measurements suggests that within a limited range of variation in growth rate, these effects tend to be small, inconsistent, and relatively less important than individual type.

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